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Phylogenetic Relationships and Classification of Exomalopsini with
a New Tribe Teratognathini (Hymenoptera: Apoidea)¹

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ABSTRACT

The phylogenetic relationships between Exomalopsini and other apine taxa and among exomalopsine groups are reexamined by means of cladistic analyses. The genera *Teratognatha* Ogloblin and *Chilimalopsis* Toro are removed from Exomalopsini and placed in a new tribe, Teratognathini. A new generic and subgeneric classification is proposed for Exomalopsini based on the results of the phylogenetic analyses. *Anthophorula* Cockerell is raised to generic status, with three subgenera: *Isomalopsis* Michener & Moure, *Anthophorisca* Michener & Moure (including *Panomalopsis* Timberlake new synonym) and *Anthophorula* s.s. *Exomalopsis* Spinola is redefined and divided into four subgenera: *Stilbomalopsis* (proposed here for *Exomalopsis solani* and related species), *Phanomalopsis* Michener & Moure, *Diomalopsis* Michener & Moure and *Exomalopsis* s.s. (including *Megomalopsis* Michener & Moure new synonym). A key is provided for the recognition of these groups.

INTRODUCTION

The tribe Exomalopsini was erected by Michener (1944) and redefined by Michener & Moure (1957) as being composed of 11 genera in 5 sections: 1. *Ancyloscelis*; 2. *Caenonoma*; 3. *Monoeca*; 4. *Exomalopsis*, *Isomalopsis*, *Teratognatha* and *Eremapis* and 5. *Chalepogenus*, *Lanthanomelissa*, *Tapinotaspis* and *Paratetrapedia*. A new genus, *Chilimalopsis*, was described by Toro (1976) and was said to be allied to *Exomalopsis*. In a recent phylogenetic study of the long-tongued bees, Roig-Alsina & Michener (1993) removed all but group 4 from Exomalopsini. Subgenera of *Exomalopsis* will be used in the sense of Michener & Moure (1957) in the following discussion, and a revised grouping will be proposed in the section on classification.

Eremapis, *Teratognatha* and *Isomalopsis* are all monospecific groups; *Chilimalopsis* contains two species. All these groups are confined to the semidesertic areas of temperate South America, which is believed to be the center of origin for Exomalopsini (Michener, 1944). *Exomalopsis*, on the other hand, is widespread through the western hemisphere, occurring in deserts, tropical savannas and forests and in temperate prairies between 41° South and 42° North. There is considerable morphological diversity in *Exomalopsis* which has been reflected in the taxonomy of the genus. Cockerell (1897b) erected the genus *Anthophorula*, which he later considered to be a subgenus of *Exomalopsis* (e.g., Cockerell, 1899). Michener & Moure (1957) recognized six subgenera (*Anthophorisca*, *Anthophorula*, *Phanomalopsis*, *Diomalopsis*, *Megomalopsis* and *Exomalopsis* s.s.). An additional subgenus, *Panomalopsis*, was erected by Timberlake (1980) to include one distinctive species.

Little is known about the biology of exomalopsine bees. Nests of the following species have been studied: *Eremapis parvula* (Neff, 1984), *Exomalopsis* (*Anthophorula*) *crenulata* (Parker, 1984), *E.* (*Anthophorula*) *torticornis* (Hicks, 1936), *E.* (*Anthophorisca*) *chiomura* (Rozen & McNeil, 1957; Rozen, 1984), *E.* (*Anthophorisca*) *consobrina* (Rozen, 1977), *E.* (*Anthophorisca*) *sidae* (Rozen, 1984), *E.* (*Phanomalopsis*) *solidaginis* (Rozen, 1984), *E.* (*Phanomalopsis*) *solani* (Linsley *et al.*, 1954; Rozen, 1984; Norden *et al.*, 1994), *E.* (*Exomalopsis*) *auropilosa* (Zucchi, 1973) and *E.* (*Exomalopsis*) *pulchella* and *E.* (*Exomalopsis*) *similis* (Raw, 1977).

Eremapis seems to construct only a single cell per nest (Neff, 1984), which suggests that it is solitary. All studied species of *Exomalopsis* s.l., on the other hand, seem to have more than one female to a nest. One nest of *Exomalopsis auropi-*

losa contained 884 females (Zucchi, 1973)! Michener (1966) suggested that cooperative provisioning may occur in *E. solani*. Raw (1977) suggested that *Exomalopsis pulchella* and *E. similis* are quasiosocial or, perhaps, semiosocial.

The foraging habits in the tribe are variable. Some species seem to be oligoleges (e.g., *Eremapis parvula* on *Prosopis* (Fabaceae)—Neff, 1984; *Exomalopsis pygmaea* on *Helianthus annuus* (Asteraceae)—Hurd *et al.*, 1980; others take their food from a wide range of plant species (e.g., *Exomalopsis auropilosa*, *E. similis*, *E. solani*—Camargo & Mazucato, 1984; Raw, 1976; Timberlake, 1980; Silveira *et al.*, 1993).

The phylogeny of the exomalopsine genera and their relationships with other bee taxa are not well understood. Exomalopsini has been considered traditionally to be among the most ancient stocks of the Anthophorinae (e.g., Michener, 1944; Michener & Moure, 1957) and to be related to the palaeartic genera *Pararhophites*, *Ancyla* and *Tarsalia* (Michener, 1944, 1979; Michener & Moure, 1957). Ideas of relatedness at the time these hypothesis were proposed, however, were commonly influenced by presence of shared plesiomorphies, and groups believed to be related then may not constitute monophyletic groups in the sense of Hennig (1966). The tribe Pararhophitini was erected by Popov (1949) for *Pararhophites*, which was later (McGinley & Rozen, 1987; Roig-Alsina & Michener, 1993) demonstrated to be part of the megachilid lineage. *Ancyla* and *Tarsalia* were grouped in the Ancylini by Michener (1944). This systematic arrangement has been generally accepted, and the question remained as to whether or not Ancylini was allied to or a synonym of Exomalopsini (e.g., Popov, 1949; Michener & Moure, 1957; Michener, 1979; McGinley & Rozen, 1987). A close relationship between the Ancylini and the Exomalopsini was supported by some of the trees obtained by Silveira (1993), but there were equally parsimonious trees in which these tribes were not sister taxa.

The first cladistic analyses to include genera of Exomalopsini were those of Roig-Alsina & Michener's (1993) study of the phylogeny of the long-tongued bees. Their results suggest that Exomalopsini would be a paraphyletic assemblage at the base of the Apinae (*sensu* Roig-Alsina & Michener, 1993; these authors do not recognize Anthophorinae as a taxon and place all genera previously assigned to it in the subfamily Apinae). In their trees, *Eremapis* was the first taxon within Exomalopsini to branch off, followed by *Teratognatha* and *Isomalopsis* plus *Exomalopsis*. In a paper com-

plementary to that of Roig-Alsina & Michener, Silveira (1993) used their data to address the relationships of Exomalopsini with other Apinae but did not reach conclusive results. His analyses suggested that Exomalopsini could either be a paraphyletic group at the base of Apinae (as in Roig-Alsina & Michener's results) or a monophyletic group with uncertain relationship to the other tribes of Apinae. *Chilimalopsis* was not included in either Roig-Alsina & Michener's (1993) or in Silveira's (1993) studies.

Here, the phylogenetic relationships between Exomalopsini and other tribes of Apinae are reexamined, and the phylogeny of the exomalopsine genera studied by means of cladistic analyses. The generic classification of Exomalopsini and the subgeneric classification of *Exomalopsis* are revised.

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MATERIAL AND METHODS

Selection of Taxa

All known species of *Teratognatha*, *Chilimalopsis*, *Eremapis* and *Isomalopsis* were included in the phylogenetic analysis. *Exomalopsis* s.l. (*sensu* Michener & Moure, 1957), however, includes some 150 species. The inclusion of all of them in this study would be impractical, not only because they would make the data matrix enormous, but also because not all of them were available for study. For this reason a sample of species was taken to represent the geographical and morphological diversity of the group. Material available for the subgenera *Exomalopsis*, *Megomalopsis* and *Planomalopsis* (*sensu* Michener & Moure, 1957) was sorted to morpho-species and identified as far as possible. During this process, the species were grouped according to the presence of features believed to be synapomorphic. From each of these groups at least two species were selected for which enough material was available for study and which would represent the geographical distribution of the groups and of the genus. The representatives of *Anthophorula* and *Anthophorisca* were chosen based on the main groups defined by Timberlake's (1980) keys. The only known species of *Diomalopsis* was also included. However, the subgeneric name *Panomalopsis* is based on a single male and, for this reason, was not included in the matrix.

The outgroups were chosen according to the findings of Roig-Alsina & Michener (1993) and Silveira (1993). Two representatives each of Ancylini, Eucerini, Emphorini, Tapinotaspini and Xylocopinae and one representative of Tetrapedini, Ctenoplectrini and Nomadinae were employed. The taxa used in the analyses are listed in Table 1.

Specimens examined for the construction of the data matrix received a green label "F.A.Silveira - Exomalopsini Relationships". Most of them are deposited at the Snow Entomological Museum of the Natural History Museum of the University of Kansas. Specimens of *Ancyla* spp., *Chilimalopsis impressifrons*, *Exomalopsis euphorbiae*, *E. completa*, and *E. sidar* are in the American Museum of Natural History, New York, U.S.A. (J.G. Rozen and E. Quinter); specimens of *Eremapis parvula*, *Isomalopsis niveata* and *Exomalopsis analis* are in the Instituto Miguel Lillo of the Universidad Nacional de Tucumán, Tucumán, Argentina (A. Willink); specimens of *Monocca* cf. *brasiliensis*, *Exomalopsis fulvofasciata*, *E. aurovilosa*, *E. analis* and *E. vernoniae* are in the Museu Regional de Entomologia da Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil (P.S.F. Fiuza); specimens of *Exomalopsis vernoniae* are in the Department of Entomology, Michigan State University, East Lansing (F.W. Stehr, V. Scott); specimens of *Exomalopsis similis*, *E. pulchella* and *Isomalopsis niveata* are in the Los Angeles County Museum of Natural History (R. R. Snelling); specimens of *Exomalopsis analis* and *E. tepaneca* are in the Museo de Zoología "Alfonso L. Herrera" of the Universidad Nacional Autónoma de México, Ciudad México, México (L. Godínez); specimens of *Exomalopsis vernoniae* are in the Museo de La Plata, La Plata, Argentina (Ricardo Ronderos); specimens of *E. aurovilosa* are in the Bee Biology and Systematics Laboratory, Logan, Utah, U.S.A. (T.L. Griswold).

Since no definitive conclusions could be reached by Roig-Alsina & Michener (1993) or Silveira (1993) about the relationships between Exomalopsini and other groups of Apinae, I preferred not to constrain the analysis to any of the specific cladograms discussed in those papers. Instead of polarizing the characters beforehand, as did Silveira (1993), I allowed the analyses to indicate the most parsimonious arrangements for Exomalopsini and the other groups, as suggested by Nixon & Carpenter (1993) and used Xylocopinae (*Manuelia* + *Xylocopa*) to root the trees.

Selection of Characters

Characters appearing in only one of the species employed in the analyses were excluded from the cladistic analyses since they would not convey phylogenetic information. Quantitative continuous characters were generally (but not completely) avoided. Coding for such characters will be discussed in the description of individual characters below.

Only characters believed to be independent of other characters were employed. The presence of yellow or white marks on face of male bees has been used as a single character. The observation that yellow marks can be independently present in different parts of the face (labrum, clypeus, supraclypeal area etc.) prompted me to divide this feature into several characters (numbers 15 - 20, below). The same was done regarding the presence and distribution of tomentum on metasomal terga 1 to 4 (characters 52 - 55, below).

Only external morphological characters were employed here. Furthermore, search for characters was limited to adult females and males, since immature stages are unknown for the large majority of species in the tribe. Many characters are present only in one sex as pointed out in their descriptions below. All characters for which no sex is specified are coded based on the female. Although they are known or presumed to be common for both sexes, this may not be true for all of them.

Explanations are needed as to how some characters were interpreted and named:

A sparse and regularly spaced line of erect hairs is present along the inner margin of the eyes in *Exomalopsis* (*sensu* Michener & Moure, 1957). This row of hairs is referred to, below, as the *paraoc-*

Table I. Taxa employed in the phylogenetic analyses. Generic and subgeneric classification of Exomalopsini according to Michener & Moure (1957).

OUTGROUPS	TETRAPEDIINI	
XYLOCOPINAE	<i>Tetrapedia clypeata</i> Friese	<i>E. (Exomalopsis) analis</i> Smith
<i>Manuelia gayi</i> (Spinola)		<i>E. (Exomalopsis) auropilosa</i> Spinola
<i>Xylocopa virginica</i> (Linnaeus)		<i>E. (Exomalopsis) bruesi</i> Cockerell
NOMADINAE	INGROUP	<i>E. (Exomalopsis) campestris</i> Silveira
<i>Nomada snowii</i> Cresson	<i>Chilimalopsis</i> sp. (from Chile)	<i>E. (Exomalopsis) mourei</i> Michener
ANCYLINI	<i>C. impressifrons</i> Roig-Alsina	<i>E. (Exomalopsis) pulchella</i> Cresson
<i>Ancyla oraniensis</i> Lepeletier	<i>Eremapis parvula</i> Ogloblin	<i>E. (Exomalopsis) similis</i> Cresson
<i>Tarsalia ancyloformis</i> Popov	<i>Teratognatha modesta</i> Ogloblin	<i>E. (Exomalopsis) tomentosa</i> Friese
EUCERINI	<i>Isomalopsis niveata</i> (Friese)	<i>E. (Exomalopsis) vernoniae</i> Schrottky
<i>Eucerinoda gayi</i> (Spinola)	<i>E. (Anthophoriscia) consobrina</i> Timberlake	<i>E. (Megomalopsis) fulvofasciata</i> Smith
<i>Melissodes agilis</i> Cresson	<i>E. (Anthophoriscia) micheneri</i> Timberlake	<i>E. (Megomalopsis) mellipes</i> Cresson
EMPHORINI	<i>E. (Anthophoriscia) pallidicornis</i> Timberlake	<i>E. (Phanomalopsis) aureosericea</i> Friese
<i>Ancyloscelis apiformis</i> (Fabricius)	<i>E. (Anthophoriscia) pygmaea</i> (Cresson)	<i>E. (Phanomalopsis) birkmanni</i> Cockerell
<i>Ptilothrix tricolor</i> (Friese)	<i>E. (Anthophoriscia) sidae</i> Cockerell	<i>E. (Phanomalopsis) byersi</i> Timberlake
CTENOPLECTRINI	<i>E. (Anthophoriscia) texana</i> Friese	<i>E. (Phanomalopsis) jenseni</i> Friese
<i>Ctenoplectra fuscipes</i> (Friese)	<i>E. (Anthophorula) albata</i> Timberlake	<i>E. (Phanomalopsis) snowi</i> Cockerell
TAPINOTASPINI	<i>E. (Anthophorula) compactula</i> Cockerell	<i>E. (Phanomalopsis) solani</i> Cockerell
<i>Paratetrapedia lugubris</i> (Cresson)	<i>E. (Anthophorula) completa</i> Cockerell	<i>E. (Phanomalopsis) solitaria</i> Brèthes
<i>Monoeca cf. brasiliensis</i>	<i>E. (Anthophorula) euphorbiae</i> Timberlake	<i>E. (Phanomalopsis) trifasciata</i> Brèthes
Lepeletier & Serville.	<i>E. (Diomalopsis) bicellularis</i>	
	Michener & Moure	

ular cilia. It is present both in female and males, although in the latter it is sometimes disguised by the long hairs on the paraocular areas.

The term vertex has been used in the bee literature just as a descriptive word referring to the dorsalmost region of the head. Working with *Exomalopsis*, however, makes it necessary to make a more precise definition for the region between the ocelli and the occiput (from here on, *postocellar region*), to avoid confusion between non-homologous structures. In most bees, the occiput and postocellar region can be distinguished by a more or less abrupt change in punctuation and pilosity. Frequently they are separated by a preoccipital ridge or carina. The meeting between the two regions may occur at the summit of the head or behind it, on the back of the head. In the Exomalopsini, the region corresponding to the vertex of most bees is bent backward and downward bringing the ocelli to the summit of the head and part or all the postocellar region to the back of the head (Fig. 1b,c). In the past, it was usual for authors to refer to the more or less sharp ridge on the summit of the head of *Exomalopsis* s.s. and *Megomalopsis* (both *sensu* Michener & Moure, 1957) as the preoccipital carina. This ridge, however, is clearly not homologous with the preoccipital carinae of other bees, since it is well before the vertex-occipital line. In fact, some Exomalopsini (e.g., *Isomalopsis niveata* and *Anthophorula albata*) have a true preoccipital carina on the back of their heads, a feature that apparently was not noticed by previous taxonomists (Fig. 1b). For this reason, I will refer to the structure on the head of *Exomalopsis* s.s. and *Megomalopsis* as the *postocellar ridge* and to

the arrangement of hairs referred to as occipital fringe by Timberlake (1980) as the *postocellar fringe*.

Medially, on the posterior margin of the propodeum, there is a special, somewhat strengthened area delimiting the articulating orifice of the propodeum (Fig. 5 *ao*) and producing the propodeal teeth described by Michener (1944). This area is here named 'propodeal crescent' (Fig. 5 *c*).

Many *Exomalopsis* have a shallow transverse depression that divides the dorsal surface of tergum I into an anterior and a posterior zone. Michener & Moure (1957) used this depression as a diagnostic character for their subgenera *Megomalopsis* and *Phanomalopsis*. This depression coincides with the premarginal line (Michener *et al.*, 1994), which separates the disc from the marginal area of the tergum (Michener, 1944; = posterior marginal depression of Camargo *et al.*, 1967; = apical depression of Timberlake, 1980). Strong evidence that the transverse depression is homologous to the premarginal line is the fact that, when present, it indicates the insertion of the intersegmental membrane on the internal surface of the tergum. This is the same for the premarginal line of other bees (Camargo *et al.*, 1967; Silveira, unpublished observations).

Descriptions of Transformation Series

The term character is used here, following Wiley *et al.* (1991), to designate the attribute of a given species (referred to by authors as character state). The set of alternative homologous characters (referred to by authors as character) is designated here as a trans-

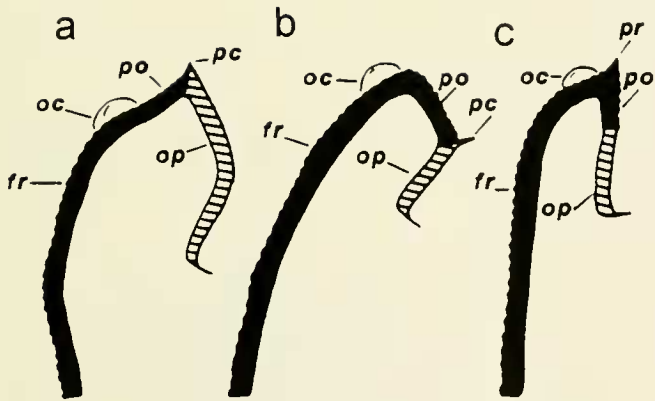


Fig. 1. Sagittal sections of heads of bees (schematic) showing hypothesized change in relative positions of postocellar region and occiput (see text for explanation). (a) as in *Monocera cf. brasiliensis*; (b) as in *Exomalopsis** (*Anthophorula*) *albata*; (c) as in *Exomalopsis* (*Megomalopsis***) *fulvofasciata*. fr = frons; oc = median ocellus; op = occiput; po = postocellar region; pc = preoccipital carina; pr = post-ocellar ridge. * *Anthophorula* in the classification proposed here. ** *Exomalopsis* in the classification proposed here.

formation series. Transformation series containing more than two characters (multistate characters of authors) were not ordered, and their numbers should not be taken to imply plesiomorphic or derived conditions. In one instance, mixed coding (as explained in Wiley *et al.*, 1991), which is a way to order characters, was employed. This was done by the use of transformation series 61 and 62 to code for variations in two of the characters in transformation series 60. Outside the ingroup, while most of the characters recorded probably do not vary greatly within any one genus, the data are based only on the exemplars listed in Table 1.

When many characters were present in a single transformation series, a detailed codification would take more than the 10 characters acceptable by parsimony programs such as Hennig86. The solution I found was to codify those characters that appeared in more than one taxon, ignoring some features occurring only in a single species among the outgroups (which were coded as the common character). The shape of disc of sternum VII of male (transformation series 60) is one example of a series in which unique characters were coded as the common feature 'triangular'. Since these unique characters would show up in the results as autapomorphies for the species in which they appear, ignoring them does not influence the topology of the cladograms obtained.

Metasomal terga and sterna are referred to, respectively, as T-1, T-2, etc. and S-1, S-2, etc.

1: Base of first labial palpomere (0) parallel sided; (1) with a constriction on inner side [Fig. 16 in Roig-Alsina & Michener, 1993].

2: Mandibles (0) simple; (1) with inner subapical tooth.

3: Posterior mandibular articulation (0) even with posterior margin of eye; (1) anterior to posterior margin of eye.

4: Disc of labrum of female (0) flat [Fig. 2a]; (1) concave [Fig. 2b]; (2) convex. *Manuelia* and *Xylocopa* have the labrum relatively reduced with a large portion represented by the basal polished area. I consider the small remaining portion, which is convex, as the disc of the labrum. I am not sure, however, of the homology relative to the labrum of other bees. *Tetrapedia* has the longitudinal median area depressed and the apical margin bent forward. Perhaps it should be considered as a different character, but I consider that the disc of the labrum is flat (coded 0). *Eucerinoda* also

has a median depression on the labrum, but the disc as a whole is not concave (coded 0).

5: Apical edge of labrum of female (0) straight or gently curved (sometimes with a median knob) [Fig. 2a]; (1) pointed [Fig. 2b]. *Tetrapedia* has a specialized labrum in which the apical edge has two median denticles (coded 0). *Eucerinoda* does have a median angle on the edge. However it looks more like a projection of the disc over the edge (like the median knob of other bees), rather than part of the edge itself (coded 0). In *Ptilothrix*, the labrum is conspicuously acuminate and is coded as such. However, the apical margin is very specialized, suggesting that it is not homologous to other pointed labra such as those in the *Exomalopsis jenseni* group. *Isomalopsis* has a relatively long labrum. The lateral portions of its apical edge do converge, but in a gentle curve, which is truncated at the apex (coded 0).

6: Longitudinal median line of female labrum (0) undifferentiated; (1) glabrous, sometimes elevated in relation to rest of disc; (2) glabrous, sometimes elevated; delimited by 2 rows of hairs [Fig. 2a]. *Eucerinoda* has a median glabrous area that is incomplete, starting far from the labral base (coded 1). In *Isomalopsis* the median line is very broad (coded 0). In *Exomalopsis birkmanni*, the two lines of hairs delimiting the median line are obliterated by a tuft of hair on each side (coded 2).

7: Anterior surface of labrum of female (0) with basal polished area; (1) without basal polished area. *Ctenoplectra fuscipes* has a thick, glabrous ridge that suggests a degenerated basal polished area. No

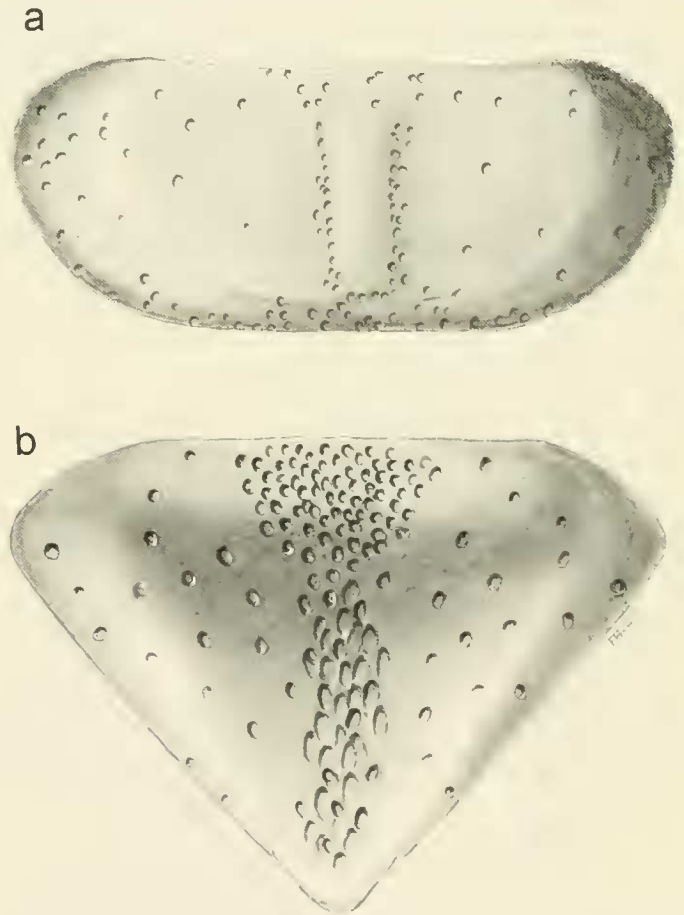


Fig. 2. Labra of (a) *E. (Exomalopsis) auropilosa* and (b) *Exomalopsis (Phanomalopsis) snovi*.

other species in the genus has it, although some others have other features suggesting the basal area (coded 0). *Teratognatha* has a flattened basal area that, for the most part, lacks punctuation. It is not much elevated and was not considered as homologous to the basal area in bees such as *Xylocopa* and *Ancyra*.

8: Outline of summit of head of female, in frontal view, (0) uniformly convex [Fig.3a]; (1) in straight line between eye and ocellus [Fig.3b]. The summit of the head in *Ancyra* is very gently convex, almost straight, but was coded as 0.

9: Lateral profile of vertex of female, between eye and lateral ocellus: (0) convex [Fig.1b]; (1) excavated [Fig.1a,c]. In *Xylocopa*, the ocelli are very low, relative to the summit of the head, and the vertex is almost level between the ocellus and the eye (coded 0).

10: Summit of head of female, in dorsal view, (0) distant from lateral ocelli (one ocellar diameter or more behind lateral ocelli); (1) close to lateral ocelli (less than one ocellar diameter behind lateral ocelli).

11: Postocellar region of female, behind summit of head, (0) convex in lateral profile [Fig.1a,b]; (1) plane or concave in lateral profile [Fig.1c]. In *Nomada*, the vertex does not bend down before meeting the occiput, but still is convex (coded 0). In *Paratetrapedia lugubris*, the summit of the head coincides with the preoccipital carina (coded 0). In *Exomalopsis aureosericea* and *E. micheneri* the postocellar region is only very gently convex, behind the summit of the head, but was still coded as 0. *Exomalopsis completa* has the postocellar region ending just behind the summit of the head. The short portion on the back of the head, however, is convex.

12: Superior margin of eye of female, in frontal view, (0) below summit of head [Fig.3a]; (1) above summit of head [Fig.3b].

13: Lateral ocelli of female, in frontal view, (0) entirely below summit of head [Fig.3a]; (1) at least partially above summit of head [Fig.3b].

14: Paraocular cilia of female (0) absent; (1) present.

15: Mandibles of male (0) entirely dark; (1) with yellow pigmented area at least at base. In most *Exomalopsini* the male mandibles are black, sometimes with parts (especially at the apex) brown to bright ferruginous. State one refers to pale to bright yellow maculae, as are sometimes found on the labrum and clypeus.

16: Labrum of male (0) entirely dark; (1) with yellow pigmented area.

17: Clypeus of male (0) entirely dark; (1) with yellow pigmented area.

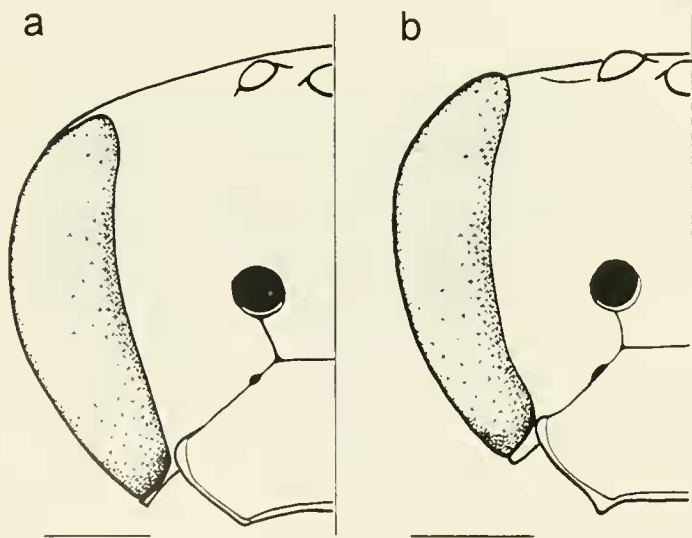


Fig. 3. Frontal views of heads of (a) *Exomalopsis (Phanomalopsis*) bukmanii* and (b) *E. (Exomalopsis) auropilosa*. Scale lines = 0.50 mm. * *Stilbomalopsis* in the classification proposed here.

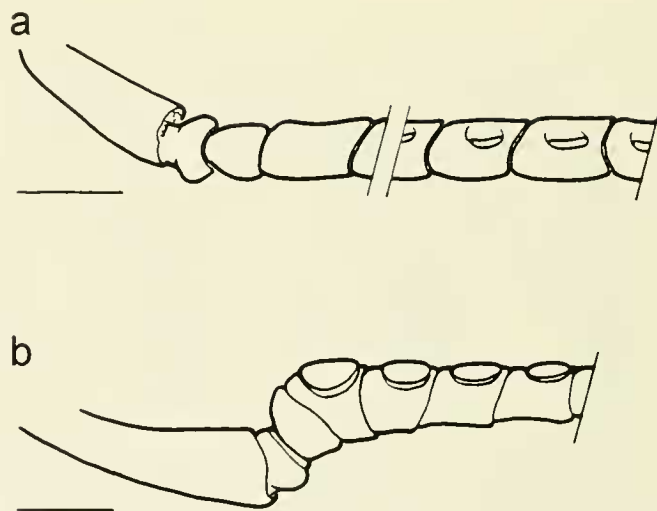


Fig. 4. Antennae of males of (a) *Exomalopsis* (Anthophorula) albata* and of (b) *Exomalopsis* (Anthophorula) completa*. Flagellomeres 3 (part), 4, 5 (part), 8 (part), 9, 10 and 11 in (a) and flagellomeres 6 (part) to 11 in (b) are omitted. Scale lines = 0.25 mm. * *Anthophorula* in the classification proposed here.

18: Paraocular area of male (0) entirely dark; (1) with yellow pigmented area.

19: Supraclypeal area of male (0) entirely dark; (1) with yellow pigmented area.

20: Scape of male (0) entirely dark; (1) with yellow pigmented area.

21: Male flagellomeres (0) entirely dark (ferruginous to black); (1) at least one yellow pigmented ventrally. *Teratognatha* has pale ferruginous flagellomeres (coded 0).

22: Male flagellomeres (0) simple; (1) with longitudinal carina on outer side [Fig.4a], which sometimes expands to form a pad [Fig.4b]. *Tetrapedia* and *Ctenoplectra* have a 'swollen' area on the line between the dorsal and ventral surfaces of the antennae. However, this does not constitute a marked edge and, thus, was coded as 0. In *Tarsalia*, the 'carina' is not very well developed but is sharply marked (coded 1).

23: Male flagellum (0) normal; (1) bulging at base, out of alignment with scape, due to an asymmetry in second flagellomere [Fig.4b].

24: First flagellomere of male (0) less than three-fourths of length of second; (1) about as long as second; (2) longer than second.

25: Posterior margin of propodeum (0) continuously separated from disc of propodeum by submarginal groove of propodeum (described by Michener, 1944) [Fig.5d,e, *sg*]; (1) compressed against disc of propodeum so that submarginal groove is interrupted at sides of propodeal crescent [Fig.5a,b]. In *Nomada*, *Melissodes* and *Chilimalopsis sp.*, there is a process of the disc of the propodeum, on each side of the propodeal crescent, which touches the posterior margin, thus interrupting the groove, which continues afterwards, in the medial part of the margin (coded 0). In *Ancyra*, the groove is closed by the propodeal crescent (coded 1).

26: Propodeal articulating orifice (0) directed backward or slightly upwards [Fig.5a,b,d, *ao*]; (1) directed downwards in an oblique plane [Fig.5d,e, *ao*].

27: Carina on posterior margin of propodeum (0) interrupted medially [Fig.5a,b,d, *c*]; (1) continuous [Fig.5c,e]. In *Xylocopa* and *Nomada* the carina looks as if it had been bent backward and downward on the sides (coded 0). Perhaps this would justify another character. In *Melissodes* the carina continues on top of the crescent as a faint wrinkle (coded 1). In *Exomalopsis similis* there

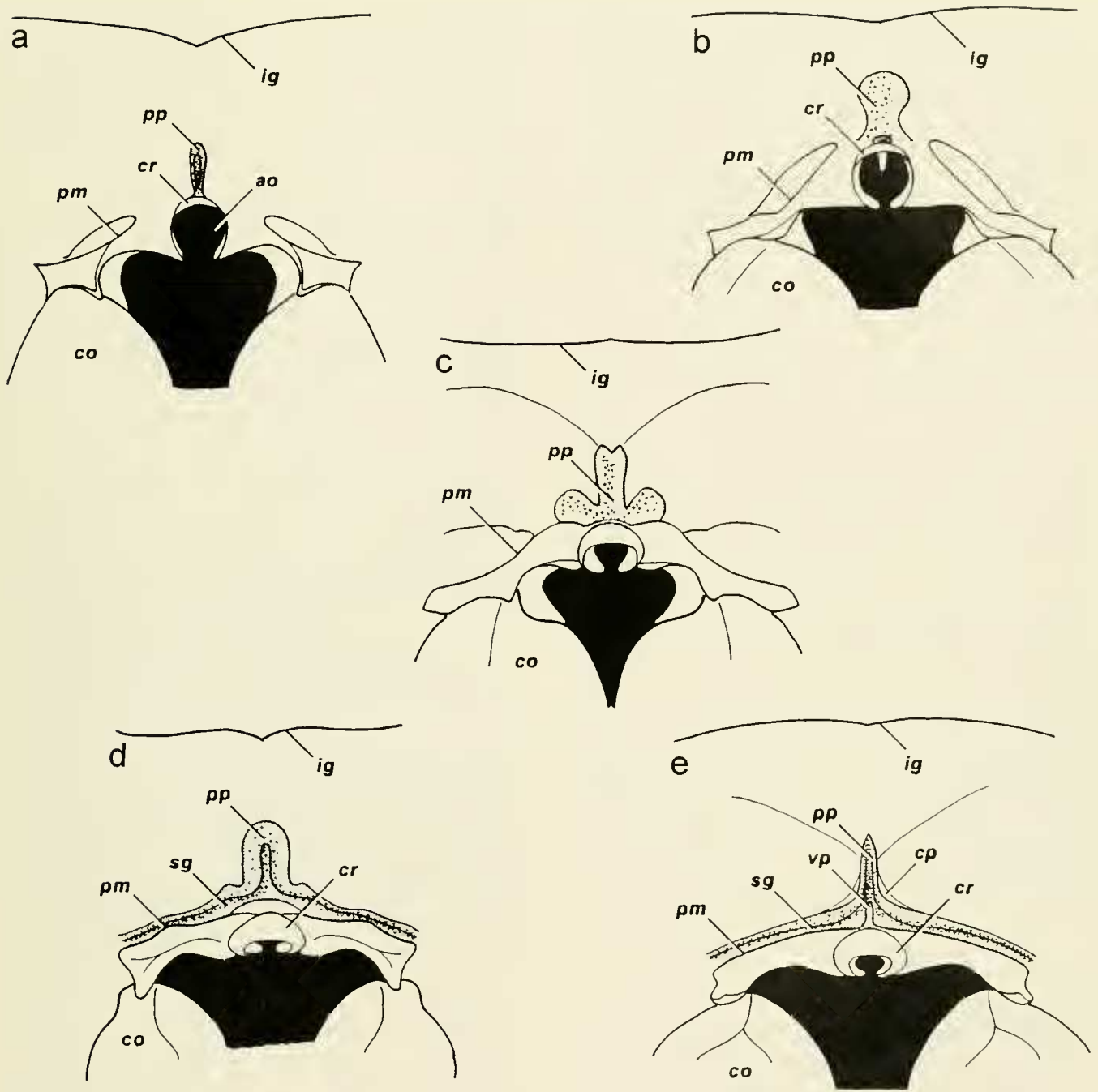


Fig. 5. Posterior view of propodeum of (a) *Paratetrapedia lugubris*; (b) *Ptilothrix tricolor*; (c) *Melissodes agilis*; (d) *Exomalopsis* (*Phanomalopsis*) *jensenii*; (e) *E. (Exomalopsis) analis*. *ao* = articulating orifice of propodeum; *co* = coxa; *cp* = lateral carina of propodeal pit; *ig* = metanotal-propodeal groove; *pm* = posterior margin of propodeum; *pp* = propodeal pit; *cr* = propodeal crescent; *sg* = submarginal groove of propodeum; *vp* = median vertical projection. Stippled areas are impressed into wall of propodeal disc.

is a very reduced line over the crescent (coded 1).

28: Carina on posterior margin of propodeum (0) simple [Fig.5c]; (1) with median vertical projection [Fig.5e, *vp*]. *Exomalopsis bruesi* and, perhaps, *Exomalopsis auropilosa* are polymorphic for this character.

29: Apical third of propodeal triangle, above propodeal pit, (0) with well delimited, shining, non-punctate area; (1) punctate as

remainder of propodeum or reticulate. In *Eremapis*, there is some faint indication of reticulation, but the surface is shiny and, to a great extent, smooth (coded 0).

30: Propodeal pit (0) broad and/or with its lateral walls gently slanting toward midline [Fig.5a,b,c,d, *pp*]; (1) a narrow groove, with its lateral walls almost perpendicular to its floor [Fig.5e, *pp*].

31: Submarginal groove of propodeum (0) not or very gently

impressed into wall of propodeal disc [Fig.5a,b]; (1) clearly impressed into wall of propodeal disc and merging with propodeal pit [Fig.5d, *sg*, *pp*]; (2) as in (1), above, but with a carina above groove on each side of propodeal pit [Fig.5e, *cp*]. In *Paratetrapedia* and *Melissodes*, the groove is deeply impressed, but only for a very short distance on each side of the propodeal crescent, not reaching the propodeal pit [Fig.5a,c] (coded 0).

32: Propodeum, in profile, (0) with a nearly horizontal basal zone, behind which it abruptly turns downward to form declivous posterior surface; (1) entirely slanting or declivous.

33: Membrane closing space behind metasternum and hind coxae and extending to base of metasomal S-1 (0) arising above free apex of metasternum on ridge between hind coxal condyles [Fig.23a,b in Roig-Alsina & Michener, 1993]; (1) arising from apical margin of metasternum, which therefore is not free [Fig.23c in Roig-Alsina & Michener, 1993].

34: Apex of marginal cell (0) on wing margin; (1) rounded or pointed, separating from wing margin in a gentle curve; (2) obliquely truncate, separating from wing margin in a straight line [Fig.6a,b]. In *Paratetrapedia* the cell first recedes from the wing margin in a gentle curve and then continues in a straight line (coded 1).

35: Inner breadth of pterostigma (0) much greater than breadth of marginal veins of pterostigma [Fig.6b]; (1) equal to or less than breadth of marginal veins of pterostigma [Fig.6a, *mv*].

36: Pterostigma (0) at least three times as long as prestigma [Fig.6b]; (1) less than three times as long as prestigma [Fig.6a].

37: Cross vein *cu-v* of forewing meeting vein *m+cu* (0) basad of or at vein *m*; (1) distal to vein *m*. The meeting of *cu-v* and *m+cu* was considered to be at *m* whenever any superposition between *cu-v* and *m* existed on *m+cu*.

38: Ventral surface of front coxa of female (0) with pilosity similar to that on rest of venter of thorax; (1) covered by densely plumose tomentum; (2) covered by thin, short, simple, decumbent hair. In *Anthophorula compactula* and *A. completa* the tomentum is not as dense as in other species (coded 1).

39: Basitibial plate of female (0) flat; (1) with central velvet-like pilose area separated by groove from raised margin.

40: Scopa on hind leg of female (0) dense, with hairs coarsely plumose to apex or nearly so; (1) dense, with mixture of long, simple hairs and shorter, plumose ones; (2) dense, constituting solely of stiff simple hairs; (3) sparse, with hairs minutely and sparsely branched. In *Ptilothrix*, the rachis of each hair is very long and stiff and its branches are very thin and restricted to the basal half of the rachis. This arrangement superficially resembles character (1) but was coded 0.

41: Hind basitarsus of female (0) giving rise to second tarsomere at apex; (1) projecting distad, above articulation of sec-

ond tarsomere, as process without an apical brush; (2) projecting distad as in (1), but ending in a dense brush (penicillus). In *Ctenoplectra*, the projection is topped by a fine, long and thin brush (coded 1). In Roig-Alsina & Michener (1993), *Paratetrapedia* is coded 1 and *Monoecca* coded 0. The species of *Paratetrapedia* I studied has the structure of the hind basitarsus very similar to that of *Monoecca* and both were coded 0. *Eremapis* is coded as 1 in Roig-Alsina & Michener's paper. My interpretation, however, is that, although very reduced, both the projection and the penicillus are present (coded 2).

42: Hind basitarsus of female (0) narrow (measured at its apex, narrower than tibia and not more than 3 times as broad as second tarsomere), more or less round in cross-section; (1) broad (as broad as or [usually much] broader than tibia and much more than 3 times as broad as second tarsomere), flat. In *Exomalopsis*, the hind basitarsus is narrow, but somewhat flat (coded 0).

43: Trunk of anterior tibial spur (0) simple [Fig.7a]; (1) with expansion at right angle to velum, curving apically into spine of malus [Fig.7b]; (2) with strong expansion at right angle to velum, ending in strong angle [Fig.7c]; (3) with strong expansion as in (2) above, but ending in spine [Fig.7d].

44: Dorsal surface of T-1 (0) clearly shorter than exposed surface of T-2; (1) about as long as or longer than exposed surface of T-2.

45: T-1 of female (0) without transverse carina; (1) with a transverse carina marking boundary between anterior vertical surface and dorsal surface. *E. micheneri*, *E. pygmaea* and *E. texana* have a weak carina (coded 1).

46: Premarginal line (0) parallel to posterior margin of tergum; (1) arching forward between dorsolateral convexities (most easily seen on T-1, but occurring also at least on T-2 and T-3). The premarginal line is not visible in *Xylocopa*. In *Tarsalia*, it is not very clear, but was coded 1. In *Ptilothrix*, it is obvious only on T-2. In *Chilimalopsis* and *Eremapis*, the arc is very subtle (coded 1).

47: Premarginal line of T-1 of female (0) simple; (1) depressed, forming transverse sulcus. In *E. albata*, *E. compactula* and *E. completa*, the marginal area is depressed (see character 48) and the premarginal line is below the level of the disc (coded 0). In *E. fulvofasciata* and *E. mellipes*, the sulcus is very weak, as compared with that in *E. byersi*, for instance (coded 1).

48: Marginal area of T-1 of female, at midline (0) at same level as disc; (1) depressed in relation to disc.

49: Disc of T-1 of female, measured lengthwise at midline, (0) longer than marginal area; (1) shorter than but not less than one-third as long as marginal area; (2) less than one-third as long as marginal area. In *Manuecia*, *Xylocopa* and *Nomada*, the premarginal line is difficult to see and the boundaries between the disc and the marginal area of the tergum are difficult to delimit (coded ?).

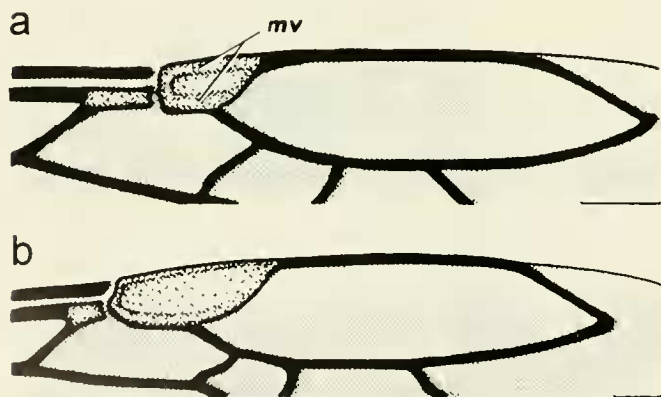


Fig. 6. Portion of front wing of (a) *Exomalopsis** (*Anthophorula*) *compactula*; (b) *E. (Exomalopsis) fulvofasciata*. *mv* = marginal veins of pterostigma. Scale lines = 0.25 mm.

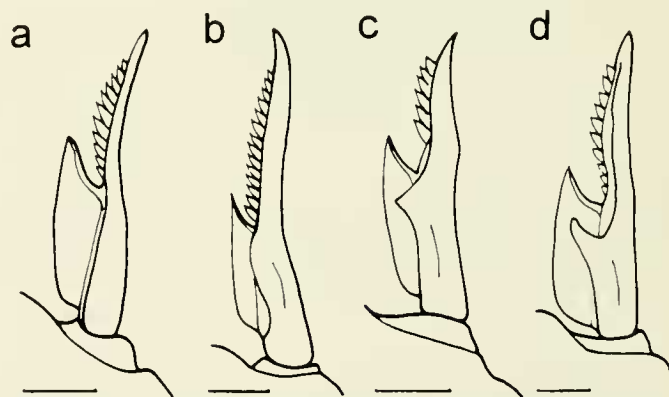


Fig. 7. Anterior tibial spur of (a) *Ancyloscelis apiformis*; (b) *Tarsalia auxyliformis*; (c) *Exomalopsis (Anthophorula) compactula*; (d) *E. (Exomalopsis) fulvofasciata*. Scale lines = 0.10 mm.

50: Disc of T-1 of female on dorsal surface, between dorsolateral convexities, (0) punctate; (1) largely impunctate, sometimes with a couple of lines of hairs close to and parallel to transverse carina. In *E. pulchella*, the premarginal line is so close to the transverse carina that there is only space for a couple of lines of hairs (coded ?).

51: Marginal area of T-1 of female, between dorsolateral convexities, (0) punctate; (1) smooth, except sometimes for rows of punctures parallel to submarginal line, producing premarginal band. In *Ancyla*, there is a smooth area behind the premarginal line, but the punctures extend beyond a premarginal band (coded 0). In *E. campestris* and *E. micheneri*, there are punctures behind the premarginal line, but they seem to belong to the premarginal band (coded 1).

52: Tomentum on marginal area of T-1 of female, between dorsolateral convexities, (0) absent; (1) present, extending to margin of tergum; (2) present, forming a premarginal band sometimes interrupted medially. *Eucrinoda* was coded 1, based on the description by Michener & Moure (1957:445), because hairs on metasoma of the specimen available to me were hard to see. In *E. fulvofasciata*, the limits of the premarginal band is disguised by the presence of a band of simple hairs that mixes with it and extends almost to the margin of the tergum (coded 2).

53: Tomentum on marginal area of T-2 of female (0) absent; (1) present, extending to margin of tergum; (2) present, forming complete band that does not extend to margin of tergum; (3) present, restricted to areas behind dorsolateral convexities. In *Ancyla*, the band originates near and extends beyond the margin of the tergum, suggesting a marginal band. A close examination shows that all hairs originate on the marginal area, not on the margin of the tergum (coded 3). In *E. fulvofasciata*, the band reaches the margin all the way across the tergum, except for a very narrow median area (coded 1).

54: Tomentum on marginal area of T-3 of female (0) absent; (1) present, extending to margin of tergum; (2) present, forming complete band that does not extend to margin of tergum; (3) present, restricted to areas behind dorsolateral convexities.

55: Tomentum on marginal area of T-4 of female (0) absent; (1) present, extending to margin of tergum; (2) present, forming complete band that does not extend to margin of tergum; (3) present, restricted to areas behind dorsolateral convexities.

56: Apical hair fringes on T-1 to T-4 of female (0) absent; (1) present, sometimes interrupted medially, especially on T-1.

57: Transverse carina of T-1 of male (0) absent; (1) present.

58: T-7 of male (0) with distinct pygidial plate; (1) with no pygidial plate, apex of tergum bearing sharp transverse carina which is continuous with lateral carina; (2) pygidial plate absent, but suggested by apical carina with recurved margin; (3) pygidial plate and apical carina absent; lateral carina of tergum absent or inconspicuous. In *E. bicellularis* the carina is very poorly developed (coded 2).

59: S-6 of male (0) uniformly flat; (1) with median elevated area that broadens toward apex of sternum, forming carina or spine at each side; (2) depressed laterally with median longitudinal convexity. The form of S-6 is highly variable. Many taxa present autapomorphic states that were all coded as 0 as explained earlier. Some examples are the following: in *Tetrapedia* the sternum is concave; in *Ancyluscelis* there is a median longitudinal depression; in *Philothrix* there is a median longitudinal elevation; in *Paratetrapedia* there is a basal elevated area that extends medially, producing a sub-apical spine.

60: Disc of S-7 of male (0) subtriangular [Fig.8a]; (1) subquadriangular, with lateral edges arcuate, closest to each other medially [Fig.8b]; (2) pentagonal, latero-apical angles bearing a lateral process [Fig.8c]; (3) bilobed, lobes much broader than long [Fig.8d]; (4) bilobed, lobes much longer than broad [Figs.3,4,18,20 in Michener & Moure, 1957]; (5) trilobed [Fig.8e]; (6) subtriangular, with basilateral expansions [Fig.8f]; (7) reduced to narrow arc; (8) bilobed, lobes separated by membranous area [Fig.8g in Michener & Moure, 1957]; (9) broad, with two flat, triangular, lat-

ero-apical projections [Fig.8g]. Some characters on the disc of S-7 were clearly derived from others and this was incorporated in the matrix by means of two extra transformation series (mixed coding of Wiley *et al.*, 1991): 61 and 62:

61: Disc of S-7 of male subtriangular, with sclerotized line continuing apodemal submarginal line (0) in gentle continuous curve or in straight line; (1) distinctly produced laterally [Fig.8a, la]. Character 1 occurs only in some *Exomalopsis* s.s.

62: Disc of S-7 of male bilobed, much broader than long and (0) with posterior margin entire; (1) with small darkly sclerotized process on posterior margin [Fig.8d, sp]. Character 1 occurs only in some *Anthophorisca*.

63: Lateral processes of disc of S-7 of male (0) absent; (1) present [Fig.8b, ll]. These processes vary in length and shape.

64: Apical process of S-7 of male (0) absent or indistinguishable from the disc; (1) present as narrow transverse sclerite fused laterally to arms of disc [Fig.8b, ap]; (2) present as complex body which bears two free basilateral lobes under ventral surface of sternum [Fig.8b, bl].

65: Mid portion of basal edge of S-8 of male (0) pointed, basal edge forming two arcs with their concavities directed basad [Fig.9a,b]; (1) straight or broadly convex, whole edge producing a single arc [Fig.9c,d,e,f,g]. In *Philothrix*, the edge is barely pointed (coded 0).

66: Disc of S-8 (0) with no longitudinal carina or the carina short, near posterior margin [Fig.9b,c,e,f]; (1) with a longitudinal carina for all or almost all sternal length [Fig.9a,d]. In *Monoeca* the spiculum continues in a line across the disc, but this is not a carina such as in *Melissodes* or *Anthophorula* (coded 0). In *Chilimalopsis* and *Teratognatha* the carina is large, reaching half or a little more than half the length of the disc (coded 0).

67: Apical process of S-8 of male (0) subtriangular; (1) long, with single broad lobe separated from disc by very short constricted stalk [Fig.9a]; (2) long, bilobed, lobes separated by deep incision [Figs.2,5,11,14,17,19 in Michener & Moure, 1957]; (3) long, bilobed, lobes not separated by deep incision [Fig.9b]; (4) produced into two long, widely separated arms attached to single base [Fig.9c]; (5) long, with two dorsal sub-apical lobules and two flat subtriangular distal lobes [Fig.9d]; (6) long, with single bare, broad lobe separated from disc by strongly constricted stalk [Fig.9e]; (7) short, sometimes with two narrow projections [Fig.9f]; (8) broad, moderately long, with median apical incision [Fig.9g in Michener & Moure, 1957]; (9) long with single, broad, flat, hairy lobe, separated from disc by long strongly constricted stalk [Fig.9g]; (10) subtriangular, long, with two narrow apical projections [Fig.45 in Michener & Moure, 1957]. In *Nylocopa*, the process is very short, almost absent (coded 0). *Nomada* has a subtriangular process, which however is modified by a folded margin that bears setae and spines (coded 0).

68: Pockets on postero-lateral margin of disc of S-8 of male (0) absent; (1) present, bent dorsad [Fig.9c, mp]; (2) present, in same plane as disc [Fig.9a, mp]. In *Eucrinoda* and *Isomalopsis* there is a folding on the margin of the disc that may not be homologous to the more complex pockets in *Tarsalia* or *Teratognatha*. However, since it is in the same position it was coded (2).

69: Internal dorsal transverse ridge of gonocoxite (0) absent; (1) present [Fig.10, dr]. *Exomalopsis solitaria* does have a ridge, but it is oriented very differently (longitudinally) from that of other *Exomalopsis* (coded 1). In *E. tomentosa* the ridge is very short (coded 1).

70: Dorsal flange of gonocoxite (0) absent; (1) present [Figs.11a, 14 df]. In *E. trifasciata* it is reduced to little more than a carina (coded 1).

71: Lateral arms of gonocoxite (0) absent or short [Fig.12 ag]; (1) long [Fig.10, ag].

72: Gonocoxite (0) without ventrolateral sulcus; (1) with oblique ventrolateral sulcus [Fig.12, vs].

73: Ventral angle of gonocoxite: (0) simple; (1) produced into narrow lobe or spine [Fig.12, sv].

74: Internal wall of arm of gonocoxite, at apex, (0) simple; (1)

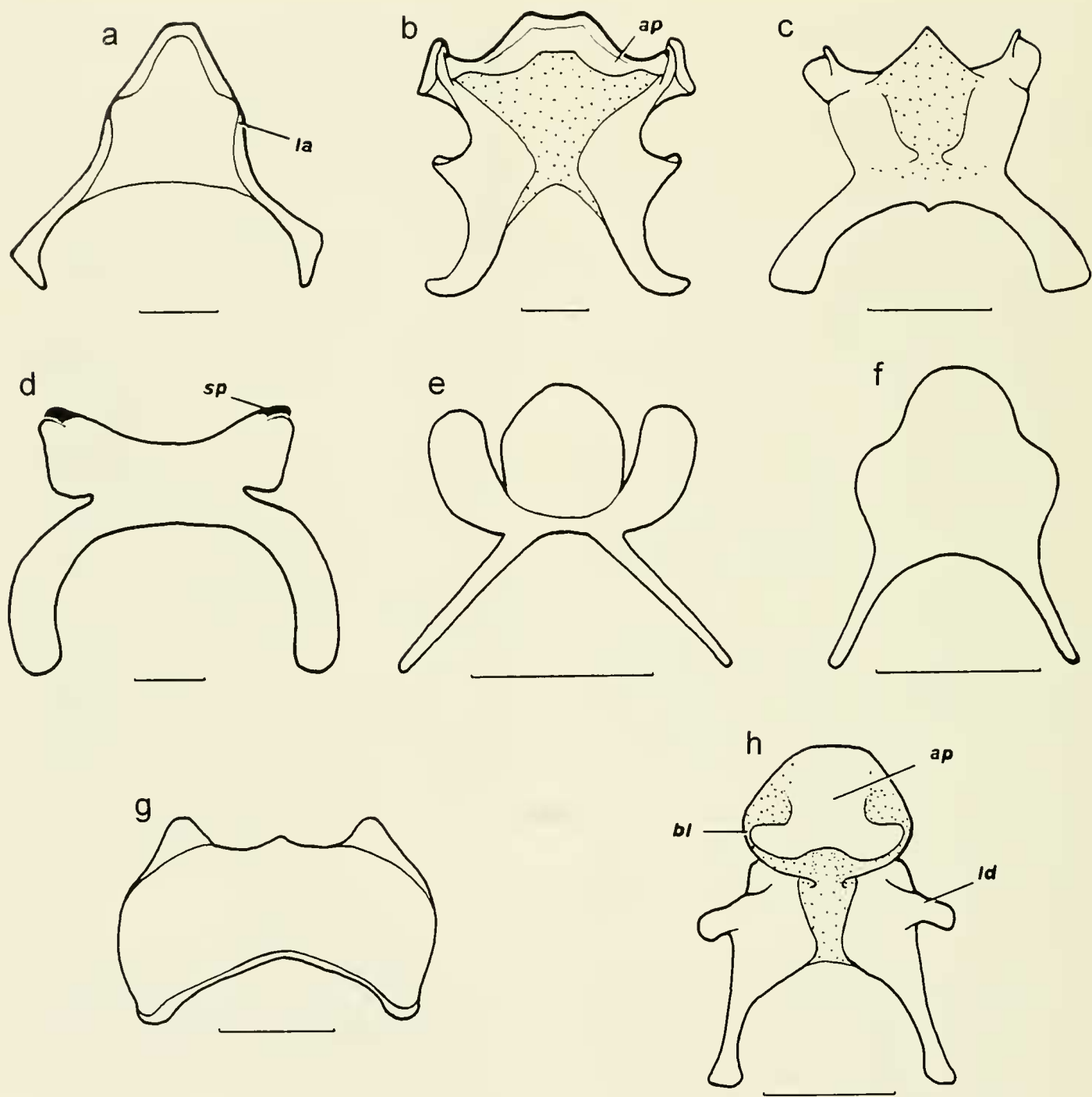


Fig. 8. Sternum 7 of (a) *E. (Exomalopsis) antipilosa*; (b) *E. (Phanomalopsis*) byersi*; (c) *Teratognatha modesta*; (d) *E. (Anthophorisca) micheneri*; (e) *Eremapis parvula*; (f) *Exomalopsis (Diomalopsis) bicellularis*; (g) *Isomalopsis niveata*; (h) *Exomalopsis (Phanomalopsis) jenseni*. *ap* = apical process of disc of S-7; *bl* = basolateral lobe of apical process; *la* = lateral production of sclerotized line of disc; *ld* = lateral process of disc; *sp* = sclerotized process of posterior margin. Hairs omitted. Stippled areas are nonsclerotized. Scale lines = 0.20 mm. * *Stilbomalopsis* in the classification proposed here.

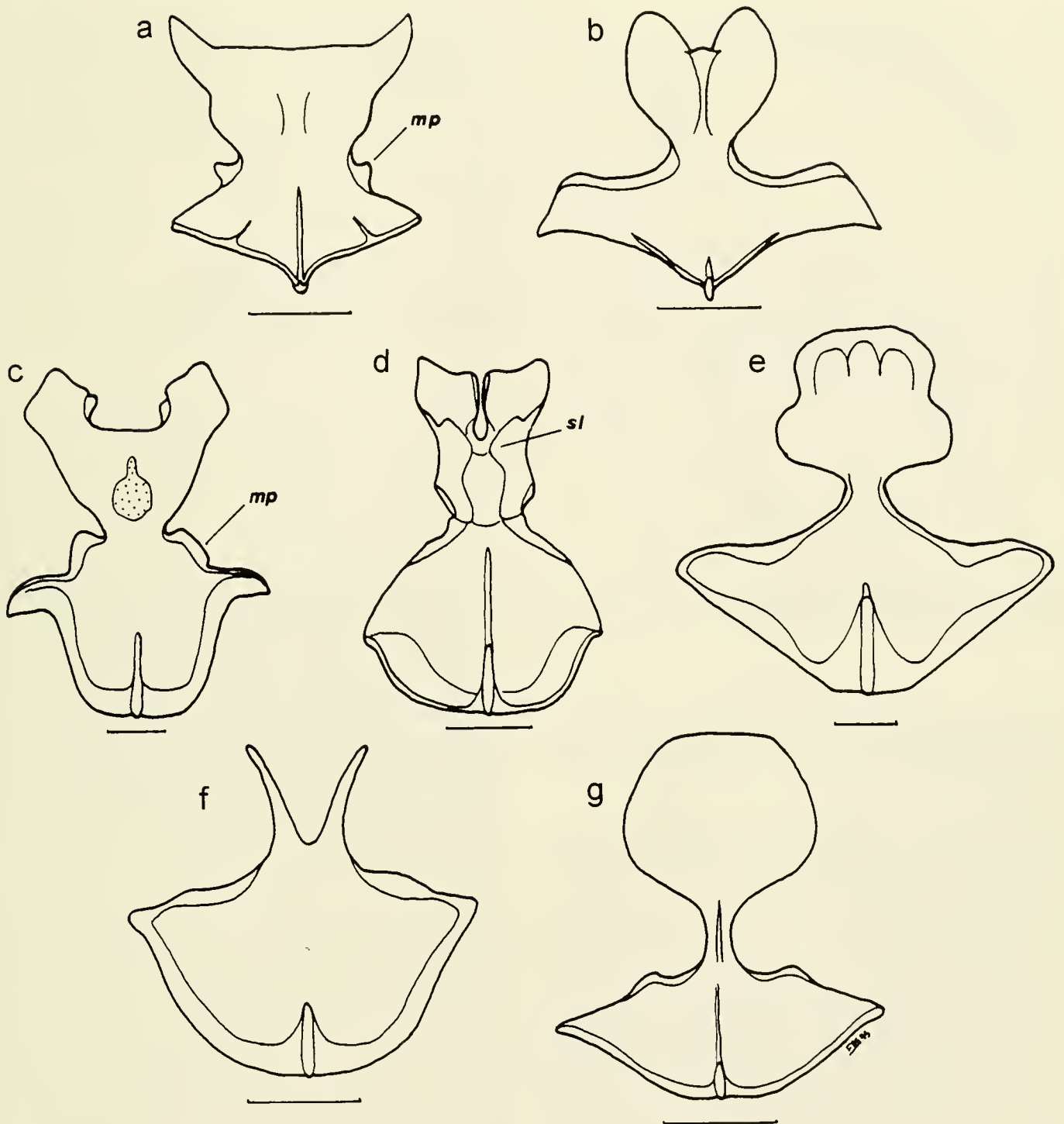


Fig. 9. Dorsal views of sternum 8 of (a) *Teratognatha modesta*; (b) *Ancyla oraniensis*; (c) *Exomalopsis* (*Phanomalopsis*) *jeuseni*; (d) *Exomalopsis** (*Anthophoriscia*) *compactula*; (e) *Exomalopsis* (*Phanomalopsis*) *byersi*; (f) *E. (Exomalopsis) auropilosa*; (g) *Exomalopsis. (Diomalopsis) bicellularis*. *mp*= marginal pocket of disc; *sl*= subapical lobes. Stippled area is nonsclerotized. Hairs omitted. Scale lines = 0.20 mm. **Anthophorula* in the classification proposed here.

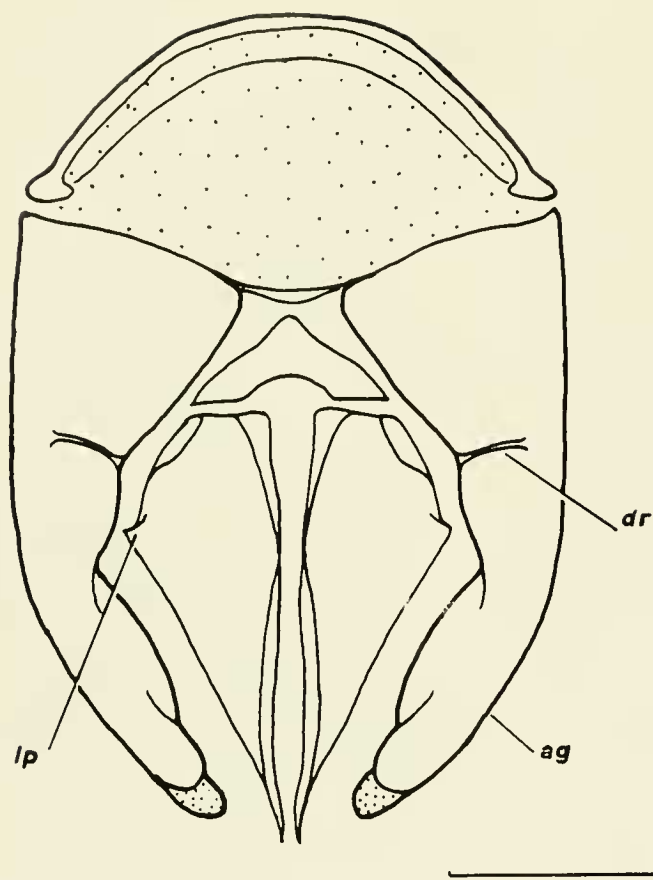


Fig. 10. Dorsal view of genitalia of *E. (Exomalopsis) auropilosa*. *ag* = arm of gonocoxite; *dr* = internal dorsal transverse ridge of gonocoxite; *lp* = lateral process of penis valve. Stippled areas are non-sclerotized. Scale line = 0.50 mm.

with narrow, dorsally directed process above gonostylus [Fig.12, *pw*]; (2) with narrow, horizontally or ventrally directed process below gonostylus [Fig.15 in Michener & Moure, 1957].

75: Peglike setae (0) absent; (1) present on subapical internal surface of gonocoxite [Fig.12, *pg*]; (2) present, on apex of gonocoxite [Fig.13b, *pg*].

76: Apex of gonocoxite (0) simple; (1) extended dorsally and ventrally, producing a median invagination that encloses base of gonostylus [Fig.14, *de,ve*]; (2) extended dorsally so that gonostylus originates subapically, beneath the extension.

77: Gonostylus (0) long, slender, sometimes with spherical apex [Figs.11,12]; (1) relatively long and slender, arising from apico-lateral process of gonocoxite at pronounced angle [Fig.15]; (2) short, triangular in profile, broader at base than at apex [Fig.14]; (3) long, flattened dorso-ventrally, originating sub-apically under arm of gonocoxite [Fig.80 in Michener & Moure, 1957]; (4) broad, broader at apex than at base, flattened dorso-ventrally, originating at tip of gonocoxite [Fig.16]; (5) absent (perhaps modified into a broad lobe? See discussion below) [Fig.13a,b]. In *Nomada*, the gonostylus is somewhat compressed laterally, but was coded as (0).

78: Ventral surface of dorsal bridge of penis valves (0) simple; (1) with median process that overhangs laterally, supporting produced basal margin of penis valve [Fig.35 in Roig-Alsina & Michener, 1993].

79: Posterior margin of dorsal bridge of penis valves, medially (0) entire, notched or with small lobe; (1) expanded into a lobe

that extends between (but not over) penis valves [Fig.11a, 17a]. In *Ctenoplectra*, the bridge is long and does extend between the penis valves, but the lobe is not produced mesally but overlaps the base of the penis valve (coded 0).

80: Base of penis valve, dorsally and behind dorsal bridge of penis valves, (0) sliding under or over dorsal bridge or touching it at a more or less perpendicular angle; (1) notched, producing a transverse plate which abuts dorsal bridge, both being on about same plane [Fig.13a, *lp*].

81: Outer side of penis valve (0) simple; (1) with lateral process [Figs.10,12 *lp*].

82: Dorsal blade of penis valve (0) absent; (1) present [Fig.13a,b *db*].

83: Ventral lobe of penis valve (0) absent; (1) present [Fig.11b *vl*].

84: Ventral surface of penis valve, subapically (0) evenly sclerotized in continuity with lateral surfaces of penis valve; (1) separated from lateral surfaces by mesal and external membranous sinuses [Fig.17b *ms,es*].

Analyses

Phylogenetic analyses were performed using the program Hennig86 version 1.5 (Farris, 1988 - provided by B. Alexander) in an IBM-compatible computer with a Cx486DLC processor. The matrix employed is shown in Table II. There, however, taxa are organized according to their relationships in the results, so that distribution of characters can be easily checked within and among clades.

To search for different islands of most parsimonious trees (Maddison, 1991), four sets of analyses were done. Before each one, the order of taxa in the matrix was changed by arbitrarily rearranging the taxa. In each set of analyses, the command *bb** was applied to trees that had been found by commands *mhennig**, *mhennig*, *hennig* and *hennig** (these commands are described in Farris, 1988). Successive approximations weighting (Farris, 1969; 1988) was then applied to the results.

In the results and discussion below, focus will be given to the relationships among the main clades, not to the relationships among species. As in Silveira (1993), some strict consensus trees will be presented in which terminal taxa belonging to monophyletic groups were collapsed ("summaries of consensus trees"). These trees will appear to be fully resolved when polytomies were restricted to the relationships among taxa within the collapsed groups. Statistics shown for the cladograms are: length (*l*), consistency index (*ci*) and retention index (*ri*).

RESULTS

Cladograms

All sets of analyses produced minimum-length trees with the same statistics (*l* = 380; *ci* = 34 and *ri* = 72) and the same main features, as shown in the summary consensus tree in Fig.18. However, not all 16 analyses (four in each of the four sets defined above) yielded exactly the same trees: five of them yielded 66 trees, seven others yielded 63 trees, three yielded 61 and one yielded 127 trees. These trees differed only by the way in which the species of *Exomalopsis s.s.* + *Megomalopsis* were arranged. The consensus trees for the first five analyses were identical and showed *E. campestris* as the basal branch for the group, with *E. mellipes* and *E. fulvofasciata* as sister-species arising from a polytomy with the other eight species of *Exomalopsis s.s.* (Fig.19a). The nine following analyses (yielding 63 and 61 trees) yielded another set of identical consensus trees (Fig.19b). In these, *Exomalopsis campestris* is the sister species of *E. mellipes*, and they arise from an unresolved clade including *E. vernoniae*, *E. analis*, *E. to-*

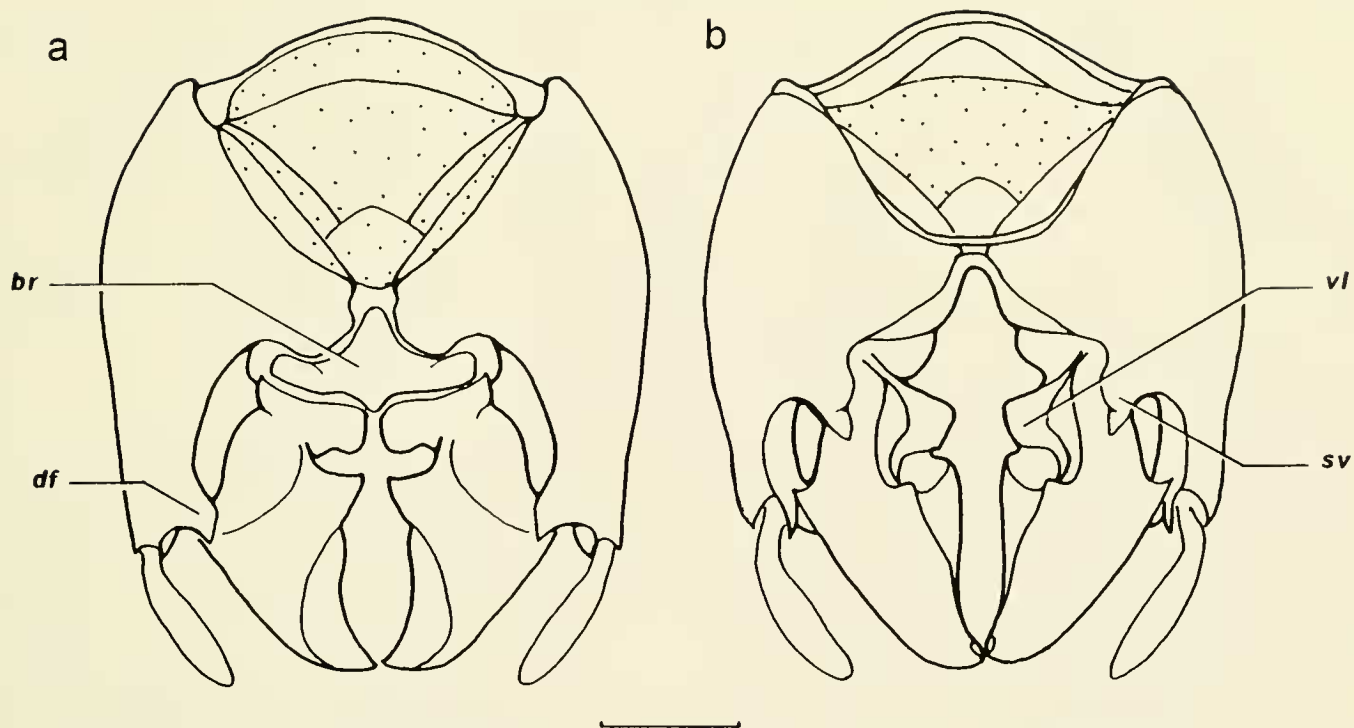


Fig. 11. Genitalia of *Exomalopsis* (*Phanomalopsis**) *solani*. (a) dorsal view; (b) ventral view. *br* = dorsal bridge of penis valves; *df* = dorsal flange of gonocoxite; *sv* = spine of ventral lobe of gonocoxite; *vl* = ventral lobe of penis valve. Scale line = 0.30 mm. * *Stilbomalopsis* in the classification proposed here.

mentosa, *E. pulchella*, *E. fulvofasciata* and *E. bruesi*. They all arise from a polytomy that also includes *E. auropilosa*, *E. similis* and *E. mourei*. The consensus tree for the analysis yielding 127 trees (Fig. 19c) shows all species of *Exomalopsis* s.s. + *Megomalopsis* arising from a single polytomy.

Successive approximations weighting for each of the 16 analyses produced different numbers of equally parsimonious trees with different statistics, depending on the number of initial trees. Some representative numbers are: $l = 824$, $ci = 65$, $ri = 89$, 1736 trees; $l = 811$, $ci = 63$, $ri = 88$, 984 trees; $l = 818$, $ci = 66$, $ri = 89$, 298 trees. The consensus trees obtained after successive approximations, however, were the same for all analyses. A summary of them is reproduced in Fig. 20. The main clades obtained before and after successive approximations are the same. After successive approximations, *Diomalopsis* is always the sister-group to *Exomalopsis* s.s. + *Megomalopsis*. When characters are given equal weight, *Diomalopsis* sometimes appears as the sister group to the *Exomalopsis solani* species-group. The characters supporting each group and the alternative relationships among them are presented and discussed below.

The following account is restricted almost entirely to the unique synapomorphies supporting the main clades. A few homoplastic characters are cited when there were reasons to suspect that they are only superficially similar to features appearing elsewhere in the cladograms, or when they are constant within the clade being discussed and not frequent outside it. The distribution of the characters can be

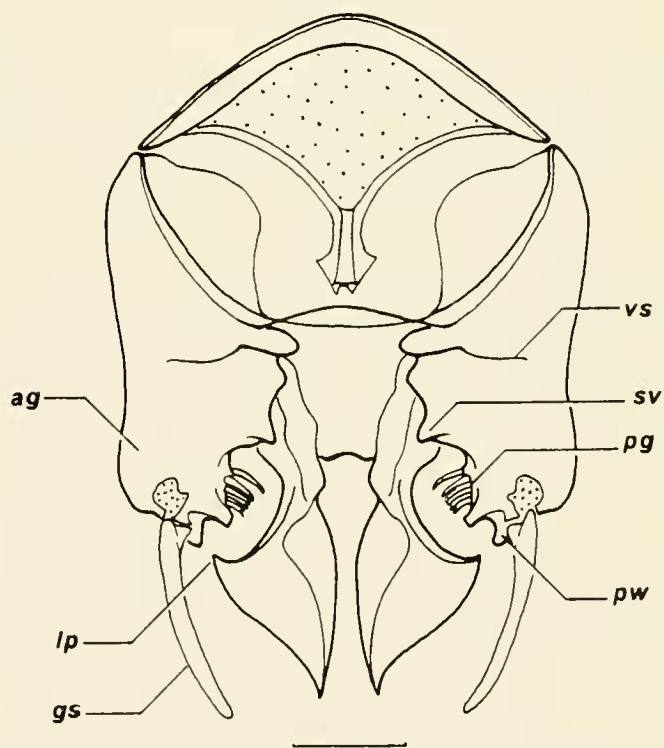


Fig. 12. Ventral view of genitalia of *Ancyla oraniensis*. *ag* = arm of gonocoxite; *gs* = gonostylus; *lp* = lateral process of penis valve; *pg* = peglike setae; *pw* = process of internal wall of gonocoxite; *sv* = spine of ventral lobe of gonocoxite; *vs* = ventrolateral sulcus of gonocoxite. Stippled areas are nonsclerotized. Scale line = 0.30 mm.

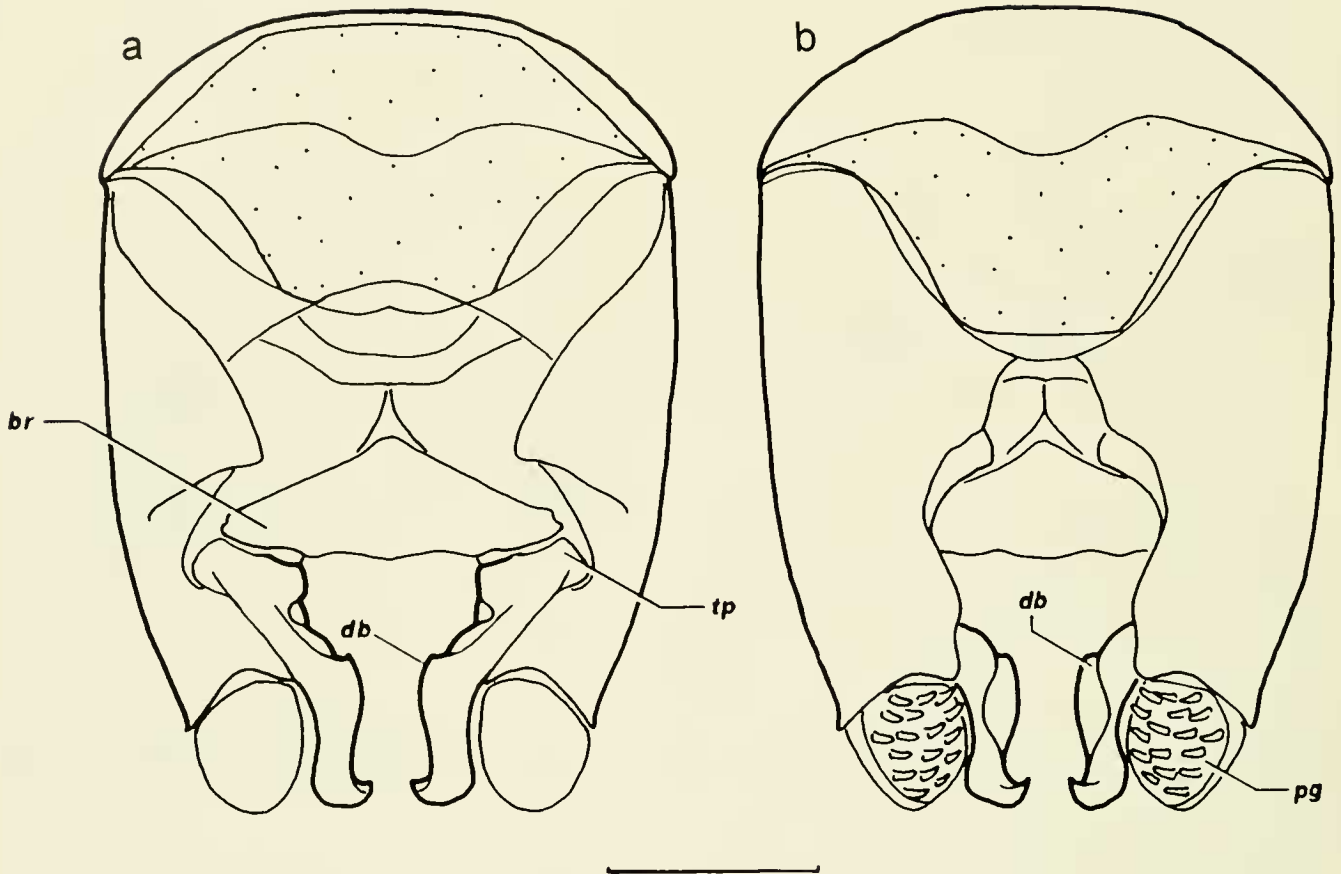


Fig. 13. Genitalia of *Exomalopsis** (*Anthophorisca*) *texana*. (a) dorsal view; (b) ventral view. *br* = dorsal bridge of penis valves; *db* = dorsal blade of penis valve; *pg* = peglike setae; *tp* = transverse plate of base of penis valve. Stippled areas are nonsclerotized. Scale line = 0.25 mm. * *Anthophorula* in the classification proposed here.

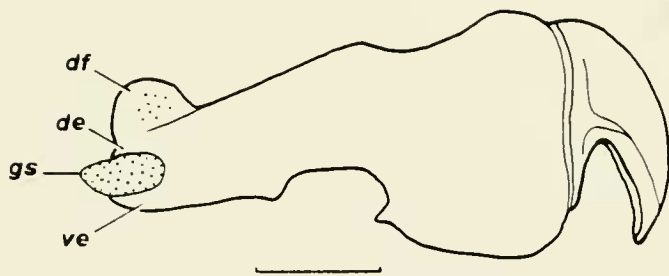


Fig. 14. Outer lateral view of genitalia of *E. (Exomalopsis) campestris* (penis valves omitted, gonobase at right). *de* = dorsal extension of gonocoxite; *df* = dorsal flange of gonocoxite; *gs* = gonostylus; *ve* = ventral expansion of gonocoxite. Stippled areas represent nonsclerotized areas in the specimen. Scale line = 0.50 mm.

checked in the trees in Figs. 21, 22 and 23, which were selected, among the many trees obtained in the several analyses, to represent alternative hypotheses for the relationships among the main lineages of Exomalopsini. The tree represented in Fig. 23 was obtained after successive approximations weighting.

Phylogenetic Relationships among the Outgroups

Conclusions about the relationships among the outgroup taxa based on the present analyses should not be overemphasized. This is because few representatives of each lineage were employed and characters were not intensively surveyed among them. It is noteworthy, however, that the relationships among the outgroups were stable throughout the analyses (Figs. 18, 20-23). Xylocopinae (represented by *Manuelia* and *Xylocopa*) and Nomadinae (represented by *Nomada*) were the first two groups to branch off, followed by Tetrapediini, and the eucerine line (as defined by Silveira, 1993).

An interesting group is the clade including the Ancylini, Eucerini and Exomalopsini (*sensu* Roig-Alsina & Michener, 1993). The only unique character common to all members of this clade is the penicillus on the hind basitarsus of females (character 41-2). The shape of the apical process of sternum VIII of male (character 67-1; Fig. 9a), which is hypothesized to be the ancestral synapomorphic condition for this clade, is actually present only in *Teatognatha* + *Chilimalopsis* and in *Eremapis*. All other lineages are characterized by alternative shapes.

This clade is divided in two broad lineages: one is com-

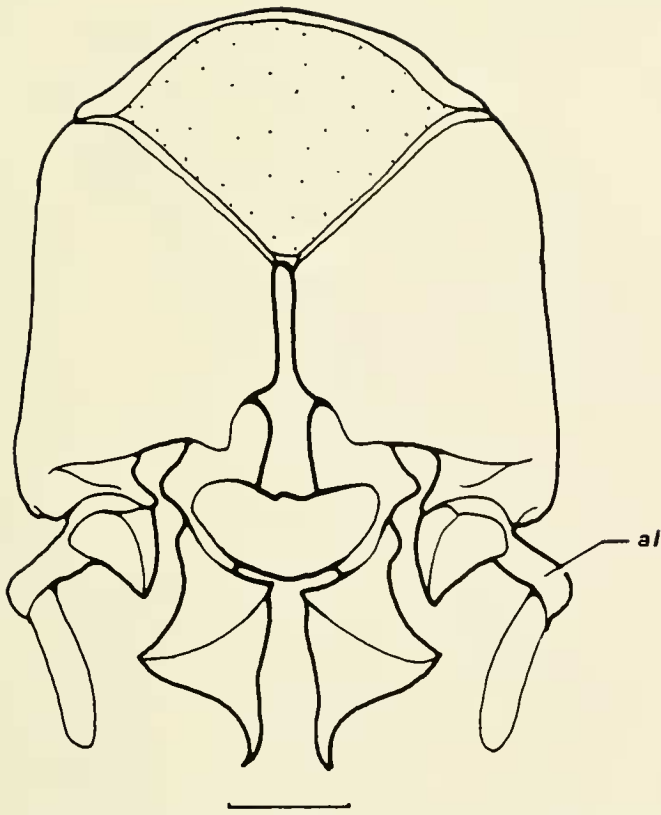


Fig. 15. Dorsal view of genitalia of *Chilimalopsis* sp. *al* = apicolateral process of gonocoxite. Stippled areas represent nonsclerotized areas in the specimen. Scale line = 0.10 mm.

prised of the Ancylini, the Eucerini and *Teratognatha* + *Chilimalopsis*; the other by Exomalopsini minus *Teratognatha* + *Chilimalopsis*. The first lineage is supported by a unique synapomorphy, the peglike setae on the subapical internal surface of the gonocoxite (character 75-1; Fig. 12, *pg*). These setae, however, are known to be present in other bees not included in the present analyses (Roig-Alsina & Michener, 1993). Other homoplastic characters supporting this clade are: the expansion of the trunk of the anterior tibial spur (character 43-1; Fig. 7b) and the process of the internal wall of the arm of the gonocoxite (character 74-1; Fig. 12, *pw*). The expansion of the anterior tibial spur has similar structure in *Ctenoplectra*. *Ctenoplectra* and *Exomalopsis aureosericea* also possess similar processes on the arm of the gonocoxite. In trees obtained after successive approximations, the narrow pterostigma (character 35-1; Fig. 6a) also appears as a synapomorphy for this clade. This also is a feature of the Emphorini and of *Anthophorula*. The monophyly of Ancylini is supported by two features: the ventrolateral sulcus of the gonocoxite (character 72-1; Fig. 12, *vs*), which was already pointed out by Silveira (1993), and a median longitudinal convexity in sternum VI of male (character 59-2). Another character supporting Ancylini is the long, bilobed apical process of sternum VIII, whose lobes are not separated by a long incision (character 67-3;

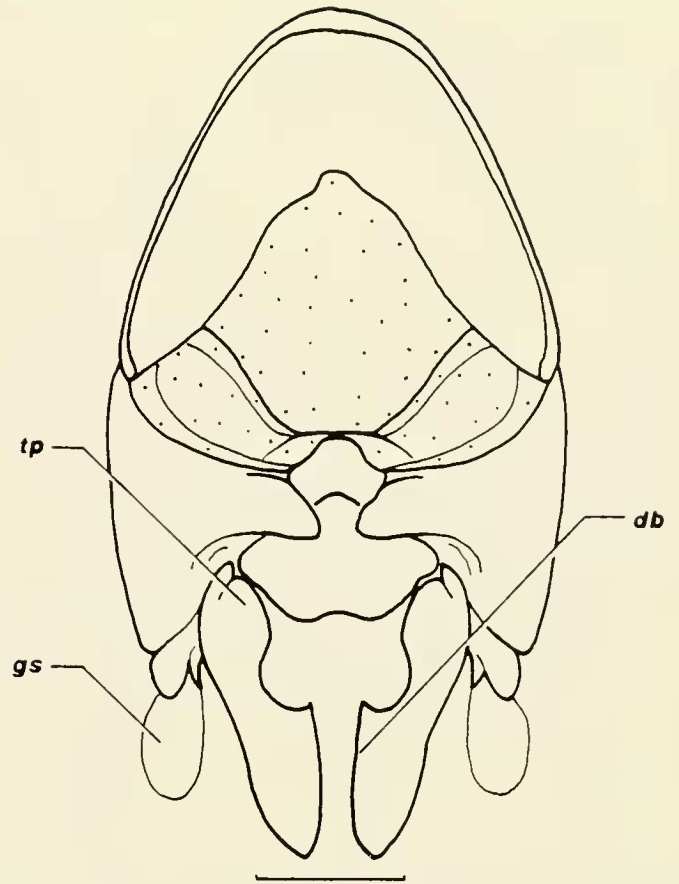


Fig. 16. Dorsal view of genitalia of *Exomalopsis** (*Anthophorula completa*). *db* = dorsal blade of penis valve; *gs* = gonostylus; *tp* = transverse plate of base of penis valve. Stippled areas represent nonsclerotized areas in the specimen. Scale line = 0.20 mm. * *Anthophorula* in the classification proposed here.

Fig. 9b). This character appears also in *Ptilothrix*. In the Ancylini, the lobes are separated by a short but wide incision, and the median longitudinal line between them is developed dorsally as a bare ridge that continues through the long basal stalk. In *Ptilothrix* the two lobes are separated apically by a narrow incision between two denticles. The median longitudinal line between the lobes is more heavily sclerotized than the rest of their surfaces (but does not constitute a ridge) and is covered by hairs. This median line does not reach the basal stalk, which is also much shorter than in Ancylini.

Under the present phylogenetic hypothesis, the genera *Teratognatha* and *Chilimalopsis* are combined in a clade that is the sister-group of the Eucerini. No unique feature supports this group and the only character supporting this clade in all trees examined is the disc of female T-1, which is longer than the marginal area (character 19-0). This character is also present in *Eremapis*, in the *Exomalopsis solani* species-group and in *Exomalopsis jenseni*. Eucerini and *Teratognatha* + *Chilimalopsis* are not very similar and the weak support their sister-group relationship receives sug-

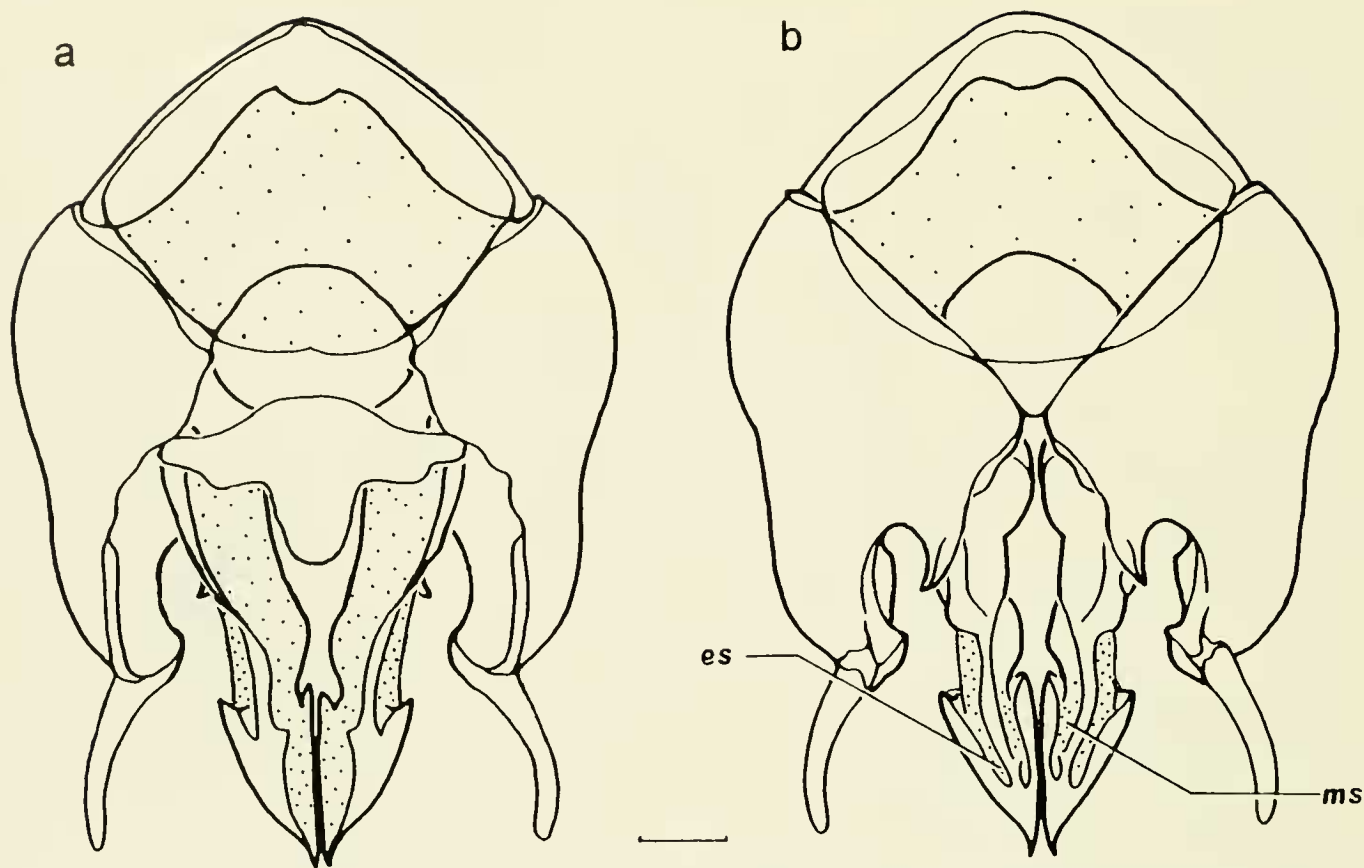


Fig. 17. *Exomalopsis (Phanomalopsis) jenseni* (male): (a) dorsal and (b) ventral views of genitalia; *ms* = mesal sinus of penis valve; *es* = external sinus of penis valve. Scale line = 0.20 mm.

gests that one should not put much confidence in this hypothesis.

The clade composed by *Teratognatha* and *Chilimalopsis* is supported by three unique synapomorphies: the ill-developed scopa composed of minutely and sparsely branched hairs (character 40-3), the pentagonal disc of S-7 of male (character 60-2; Fig. 8c) and a relatively long and slender gonostylus, which arises from the apicolateral process of the gonocoxite at a pronounced angle (character 77-1; Fig. 15). An interesting homoplastic character supporting this clade is the pockets of the posterolateral margin of the disc of S-8 of the male (character 68-2; Fig. 9a, *mp*). This character is also present in *Eucerinoda* and *Isomalopsis*, but in those genera the pockets do not protrude out of the margin of the sternum, as they do in *Teratognatha* and *Chilimalopsis*. The results show *Chilimalopsis* as a paraphyletic assemblage in relation to *Teratognatha*.

The relationships of *Teratognatha* and *Chilimalopsis*, as described above, make Exomalopsini (as defined by Roig-Alsina & Michener, 1993) polyphyletic. Exomalopsini, thus, should be limited to the genera *Eremapis*, *Isomalopsis* and *Exomalopsis* (*sensu* Michener & Moure, 1957). A single unique synapomorphy supports the tribe under this definition: a glabrous, median, longitudinal line delimited by two rows

of hairs on the labrum of females (character 6-2; Fig. 2a). Other characters supporting this clade are: the obliquely truncate apex of the marginal cell (character 34-2; Fig. 6a,b) and the long pterostigma (character 36-0; Fig. 6b—reduced in *Anthophorula s.s.*). Character 34-2 is present also in *Ancyloscelis*, *Teratognatha modesta* and *Chilimalopsis impressifrons*. Character 36-0 is present in Tapinotaspini, and in many groups outside the eucerine line.

Phylogenetic Relationships within Exomalopsini

Eremapis appears as the basal lineage of Exomalopsini (as defined above) both when characters are equally weighted and after successive approximations. Six other main lineages are defined in both analyses: *Anthophorula* + *Isomalopsis*, *Anthophorisca*, the *Exomalopsis solani* species-group of *Phanomalopsis*, *Phanomalopsis* (excluding *E. solani* and related species), *Diomalopsis* and *Exomalopsis s. stricto* + *Megomalopsis*. These lineages share three unique features: the paraocular cilia (character 14-1); the dense tomentum on the ventral surface of the frontal coxa of females (character 38-1) and the short apical process of S-8, which sometimes bears two narrow projections (character 67-7; Fig. 9f). The paraocular cilia are a unique feature among bees and are present in

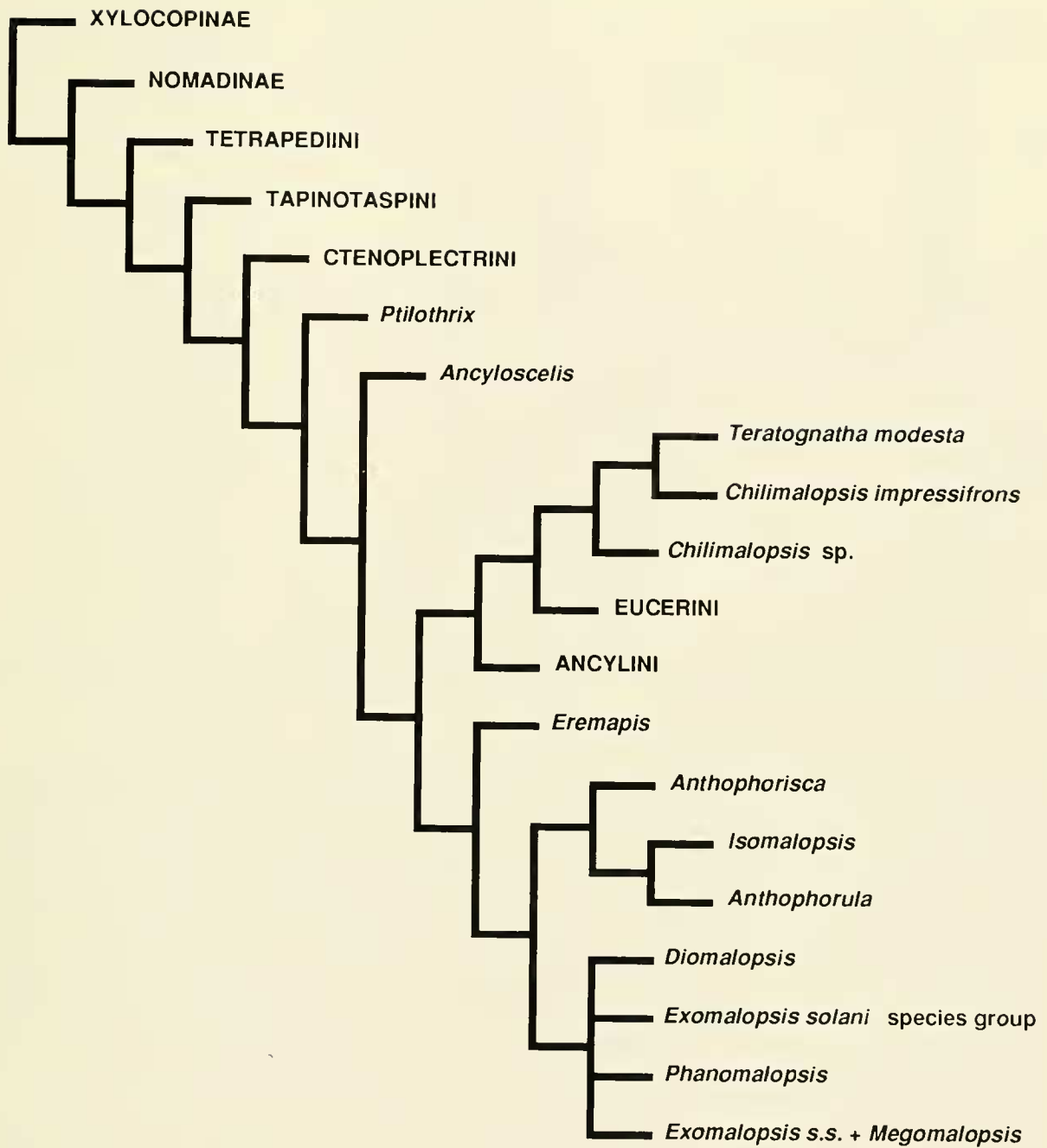


Fig. 18. Summary of the consensus tree for 1081 trees ($l = 379$; $ci = 34$; $ri = 72$) resulting from the analyses with equally weighted characters. *Exomalopsis solani* and the other species in its group were hitherto considered to be in the subgenus *Phanomalopsis*.

all examined species of *Exomalopsis* (*sensu* Michener & Moure, 1957). The pilosity on the front coxae of the females is also very distinctive. In *Anthophorisca* it is changed from dense tomentum to decumbent minute simple hairs. The apical process of S-8 of the male also varies among three groups within this lineage: *Phanomalopsis*, *Exomalopsis solani* species-group and *Diomalopsis*.

In anticipation of the taxonomical changes proposed

below, *Exomalopsis s.s. + Megomalopsis* and the *Exomalopsis solani* species group will be referred to henceforth as *Exomalopsis s.s.* and *Stilbomalopsis*, respectively.

No unique synapomorphy supports *Anthophorula+Isomalopsis*. Homoplastic characters supporting this clade are the expansion of the trunk of the anterior tibial spur, which ends in a strong angle (character 43-2; Fig. 7c) and the transverse carina on T-1 of males (character 57-1). Character 43-2 is

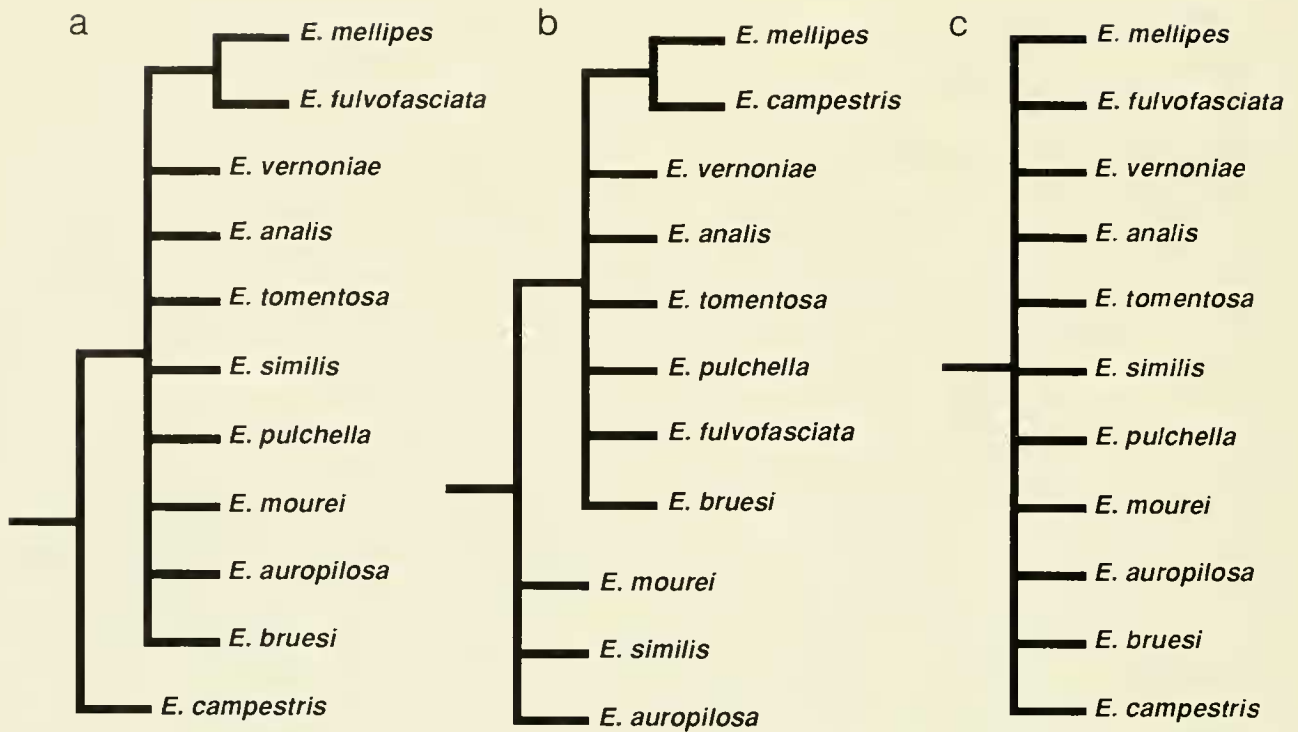


Fig. 19. Different topologies (a, b and c) within the branch shown as *Exomalopsis* s.s. (including *Megomalopsis*) in the consensus tree in Fig.18. Each of the different topologies is the outcome of one or more of the 16 analyses performed with equally weighted characters.

unique within the Exomalopsini, but also occurs in Tapinotaspini; character 57-1 appears also in *Exomalopsis jenseni*.

Some of the homoplastic features supporting the monophyly of *Anthophorula* s.s. are the reduced stigma (characters 35-1 and 36-1; Fig.6a) and the presence of a distinct pygidial plate in the males (character 58-0). These are unique features among the Exomalopsini which, however, occur elsewhere among the outgroups. Although no unique character was found to be present in all *Anthophorula* s.s. there are two unique synapomorphies for all *Anthophorula* s.s., except *A. euphorbiae*. Since this is a minute species, the absence of these features may be consequence of size reduction. The putative synapomorphies shared by the other *Anthophorula* s.s. are: the marginal area of T-1 of female, which is depressed in relation to the disc (character 48-1) and the structure of the apical process of S-8 of males, which possesses two dorsal sub-apical lobes and two flat, subtriangular distal lobes (character 67-5).

Anthophorisca is supported by two unique synapomorphies. One is the presence of the short, fine, decumbent hairs on the ventral surface of the front coxae of females (character 38-2), which is a modification of the tomentum that covers this surface in all other Exomalopsini (as defined above), except *Eremapis*. The other unique synapomorphy is the presence of peglike setae on the internal surface of the apex of the gonocoxite. Another character supporting the monophyly of this group deserves some discussion. I originally interpreted the lobe at the apex of the gonocoxa of *Anthophorisca*, not as the gonostylus, but as the parape-

lobe (Roig-Alsina & Michener, 1993), and I coded the gonostylus as absent (character 77-5; Fig.13a,b). My interpretation was based on the presence of the peglike setae, which I considered to be homologous with those present in Ancylini, Eucerini and *Teratognatha* + *Chilimalopsis*. The tree topologies obtained in the parsimony analyses, however, suggest that the peglike setae are *de novo* acquisitions of *Anthophorisca*. If this is the case, the lobe at the apex of the gonocoxa in this group may be a unique transformation of the gonostylus and thus an additional strong support for its monophyly. If the first hypothesis is correct, the absence of a gonostylus would probably be a good synapomorphy for the group, since the only other taxon included in this study that lacks a gonostylus is *Xylocopa*.

In the cladograms, the monophyly of *Anthophorula*+*Isomalopsis*+*Anthophorisca* is supported by a unique synapomorphy: the shape of the disc of S-7 of male, which is bilobed with the lobes broader than long (character 60-3; Fig.8d). This is changed in *Isomalopsis* to a broader structure with two apicolateral, flat, triangular projections (character 60-9; Fig.8g). An alternative interpretation of the homologies between these two arrangements would be to consider the broad structure in *Isomalopsis* as an enlargement of the apodemes and the triangular projections as reduced lobes. Additional support for this clade would be the transverse basal plate and the dorsal blade of the penis valves (characters 80-1 and 82-1; Figs.13a, *tp* and 13a,b, *db*). These characters would have been lost by *Isomalopsis*. Additional steps are not required in the cladograms for the accep-

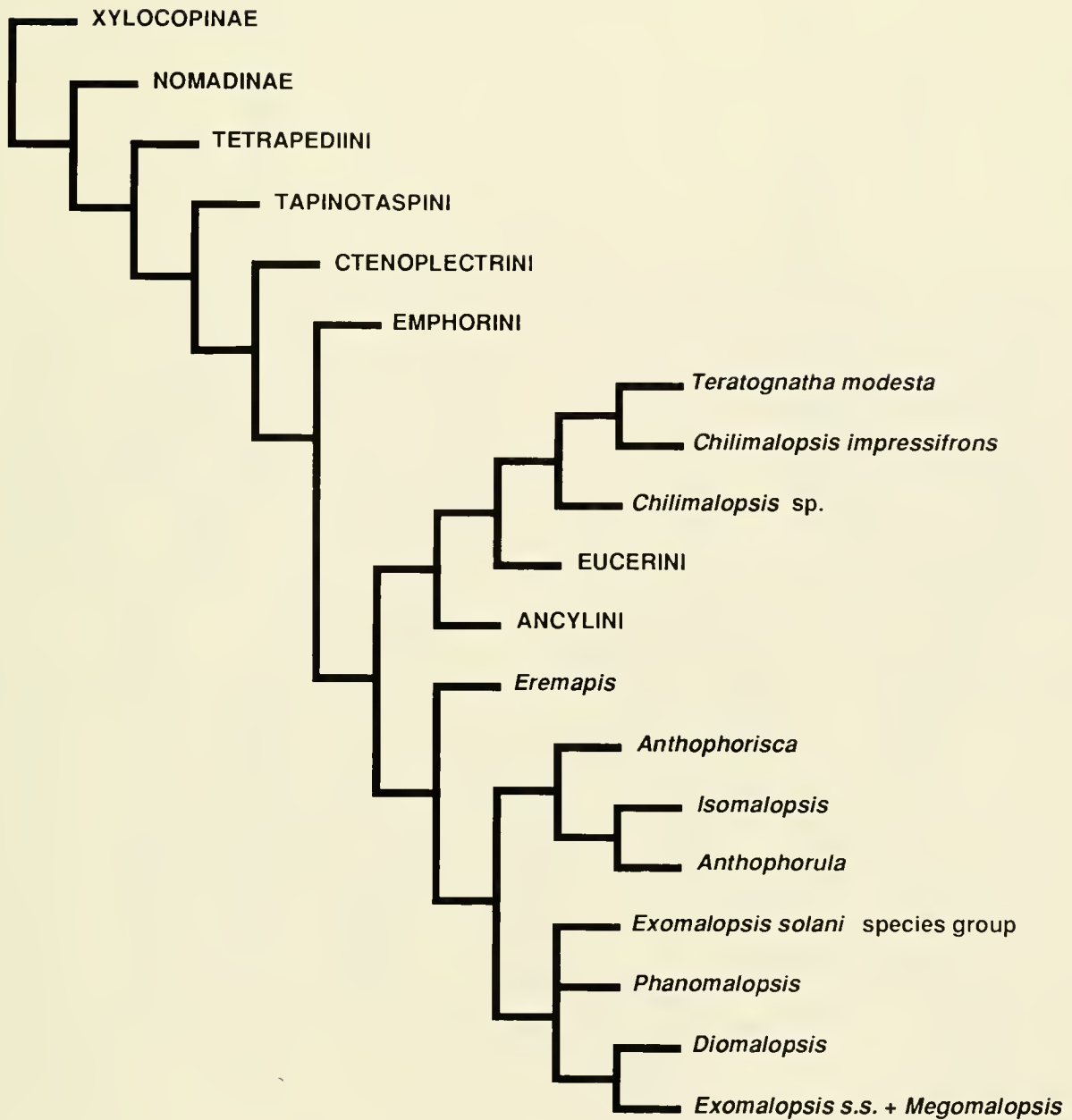


Fig. 20. Summary of the consensus trees for all analyses after successive approximations weighting. Different analyses produced different numbers of trees with slightly different statistics, but all resulted in this same consensus tree.

tance of this last hypothesis.

The analyses presented here indicate that the subgenus *Phanomalopsis*, as defined by Michener & Moure (1957), is not a monophyletic assemblage, but instead contains two independent lineages. One, *Phanomalopsis s.s.*, is composed mainly of South American species and contains the type species of the subgenus, *E. jensei*. The other lineage, *Stilbomalopsis*, is a very distinctive group of species (*E. solani* being the most common) which is mostly restricted to the semi-desertic areas of Mexico and the southwestern United States.

A single unique synapomorphy supports the monophyly

of *Phanomalopsis s.s.*: the complex (but variously modified) apical process of S-7 of the male, which bears two free basilateral lobes under its ventral surface (character 64-2; Fig. 8h, b). One of the homoplastic characters supporting this clade is the two long, widely separated arms of the apical process of S-8 of males (character 67-4; Fig. 9c). This character may indeed be a good synapomorphy for this clade. It appears again only in *Anthophorula euphorbiae*. In this species it is not so developed and may be the result of the simplification of the specialized process of other species of *Anthophorula s.s.* It should be mentioned, on the other hand, that in *Exoma-*

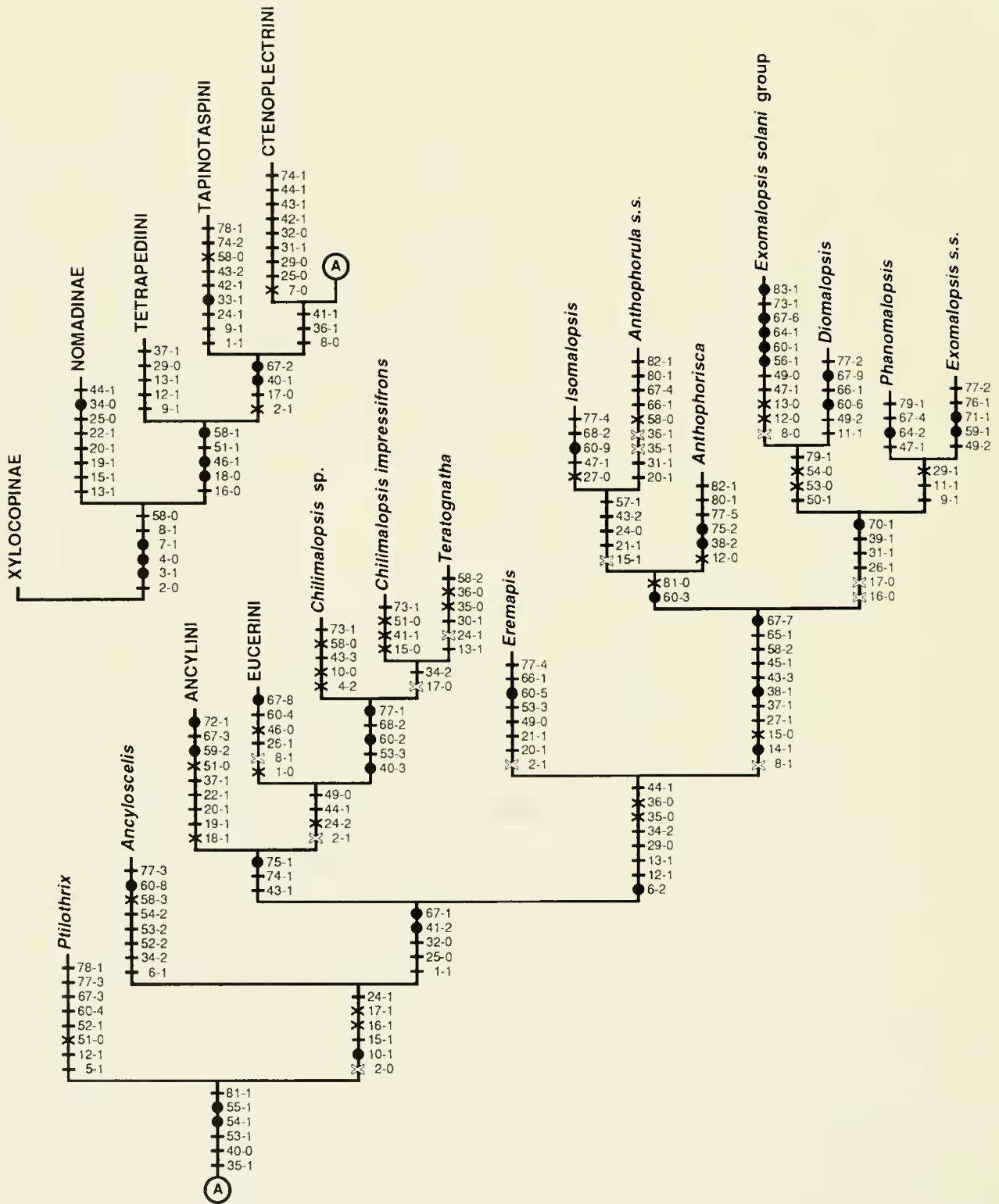


Fig. 21. Phylogenetic relationships of Exomalopsini. Example in which *Diomalopsis* is the sister-group of the *Exomalopsis solani* species group (= *Stilbomalopsis* in the classification proposed here), and *Phanomalopsis* is the sister-group of *Exomalopsis* s.s. (including *Megomalopsis*) (I = 380; ci = 34; ri = 72). Bars indicate changes that occur independently elsewhere in the tree; black crosses indicate reversals; white crosses indicate re-reversals and dots indicate changes occurring only once on the tree. The base of the tree is at the upper left.

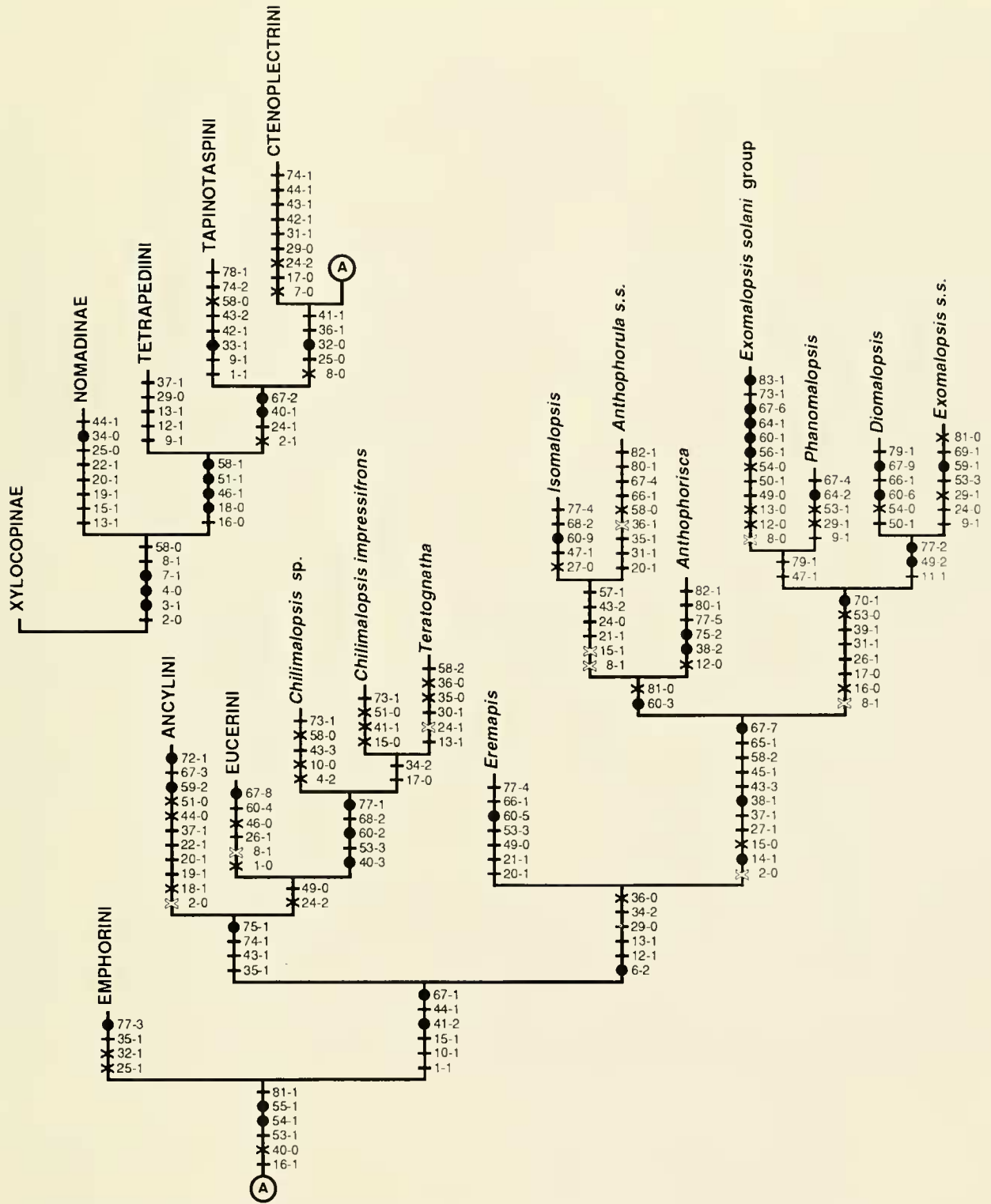


Fig. 22. Phylogenetic relationships of Exomalopsini. Example in which *Diomalopsis* is the sister-group of *Exomalopsis* s.s., and *Phanomalopsis* is sister to the *Exomalopsis solani* species group (= *Stilbomalopsis* in the classification proposed here) and *Diomalopsis* + *Exomalopsis* s.s. (including *Megomalopsis*) (l= 380; ci = 34; ri = 72). Symbols as in Figure 21. The base of the tree is at the upper left.

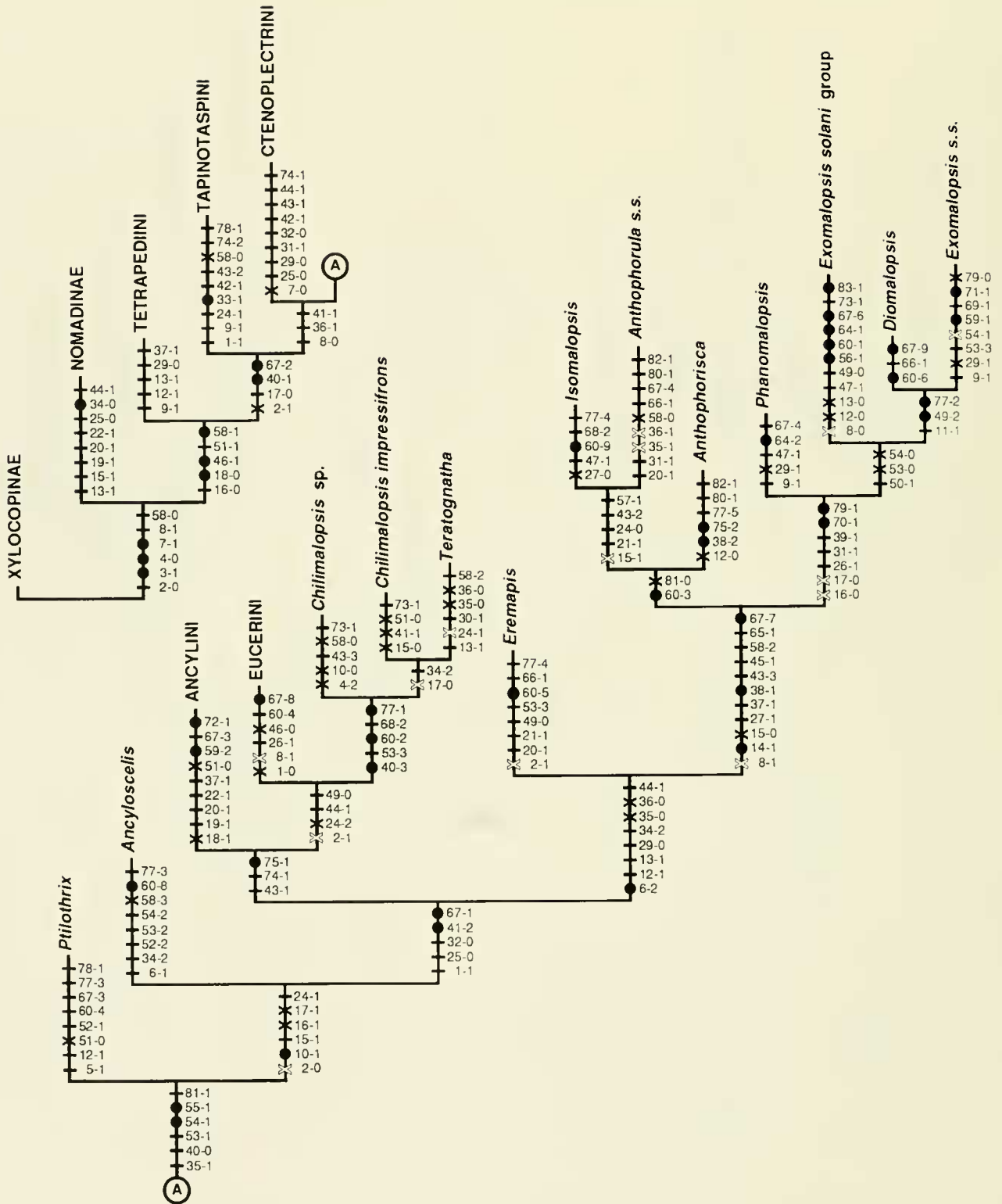


Fig. 23. Phylogenetic relationships of Exomalopsini. Example in which *Diomalopsis* is the sister-group of *Exomalopsis* s.s. (including *Megomalopsis*) and *Phanomalopsis* is sister to the *Exomalopsis solani* species group (= *Stilbomalopsis* in the classification proposed here). One of 1736 trees obtained after successive approximations weighting (1 = 824; ci = 65; ri = 89). Symbols as in Figure 21. The base of the tree is at the upper left.

Table II. Data matrix employed in the phylogenetic analyses. Numbers in italics are the character numbers as given in the text.

	1	2	3	4	5	6	7	8	
	<i>123456789</i>	<i>0123456789</i>	<i>0123456789</i>	<i>0123456789</i>	<i>0123456789</i>	<i>0123456789</i>	<i>0123456789</i>	<i>01234</i>	
<i>Manuelia</i>	110200000	0000001110	0000110001	0010100000	010000000?	0000000030	0000010000	0000000000	00000
<i>Xylocopa</i>	0102?0000	0000001111	0000210001	0010111090	200000?00?	0000000030	7000000000	0000000500	00000
<i>Nomada</i>	001000110	0001011111	1010200001	0010000000	?00010000?	0000000000	0000000000	0000000000	00000
<i>Tetrapedia</i>	001000111	0011000100	0000210000	0010100100	2000001001	0100000010	0000000000	0000000000	00000
<i>Paratetrapedia</i>	110000111	0000011100	1000110001	0011100000	1012001001	00?0000030	4000000200	0000200010	01000
<i>Monoeca</i>	111000111	0010000000	0000110001	0011100000	1012001001	1100000000	0000010?00	0000200010	00000
<i>Ctenoplectra</i>	011000000	0000000000	0000200000	0100101000	1111101001	0100000010	0000000200	0000100000	00000
<i>Ancyloscelis</i>	001001100	1000011100	0000110001	0010211000	0100001001	0122210030	8000000200	0000000300	01000
<i>Ptilothrix</i>	011010100	0010000000	0000210001	0010111000	0100001001	0011110010	4000000300	0000000310	01000
<i>Ancyla</i>	100000000	0000010111	1010110000	0000101100	0201001001	00?3110002	0000000300	0011110000	01000
<i>Tarsalia</i>	101000110	1000011111	1010100001	0000111100	0201011001	0011110012	0000000310	0010110000	01000
<i>Eucarinoda</i>	011001110	1000010111	0000201000	0000111000	0201100000	001111001?	4000001820	0000110000	01000
<i>Melissodes</i>	001000111	1000011100	0000001101	0000111000	0201110000	0102210000	4000010800	0000010000	01000
<i>Teratognatha</i>	111000100	1001011000	0000100001	1000100000	3201101000	0103110020	2000000120	0000110100	01000
<i>Chilimalopsis</i>	?11200100	0000011100	0000200001	0000011000	3203101000	0103110000	2000000120	0001110100	01000
<i>C. impressifrons</i>	111000100	1000001000	0000200001	0000011000	3101101000	0003110010	2000000120	0001110100	01000
<i>Eremapis</i>	111002100	1011011100	1100100000	0000200000	0200101000	0103110010	5000001100	0000000400	01000
<i>Isomalopsis</i>	101002110	1011111100	0100000000	0000200110	0202111101	0101110120	9000010720	0000000400	00000
<i>euphorbiae</i>	101002100	1001111100	1100000100	0100211110	0202111001	0101110100	3000011400	0000000000	10100
<i>albata</i>	101002110	1?11111100	1110000000	0100211110	0202111011	0121110120	3000011500	0000200000	10100
<i>compactula</i>	101002110	1011111101	1111000101	0000211110	0202111011	0011110100	3000011500	0000000400	10100
<i>completa</i>	101002110	1011111101	1111000101	0000211110	0202111011	0011110100	3000011500	0000000400	10100
<i>pygmaea</i>	101002110	1001101100	0000100100	0000200120	0203111001	0101110020	3000010700	0000020500	10100
<i>sidae</i>	100002100	1001101100	0000100100	0100200120	0203101001	0103110020	3000010700	0000020500	10100
<i>micheneri</i>	101002100	1001101100	0000200100	0100200120	0203111001	0121110020	3010011700	0000020500	10100
<i>texana</i>	101002100	1001111100	0000100100	0100200120	0203111001	0101110020	3010011700	0000020500	10100
<i>consobrina</i>	101002100	1001111100	0000100100	0000201120	0203111001	0001110020	30?00?00?0	0000020500	10100
<i>pallidicornis</i>	101002100	1101111100	0100100100	0000211121	0203111001	0001110020	3010011700	0000020500	10100
<i>solani</i>	101002100	1000100000	0000101100	0100200111	0203111100	1100211020	1000110600	1001000001	01010
<i>birkmanni</i>	101002100	1000100000	0000101100	0100200111	0203111100	1100011020	1000110600	100100000?	01010
<i>byersi</i>	101002100	1000100000	0000000100	0100200111	0203111100	1100011020	1000110600	1001000001	01010
<i>solitaria</i>	101002111	1111100000	0000101101	0100200111	0203111101	0101110020	0000210401	1000100001	01000
<i>aureosericea</i>	101002111	1011100000	0000001101	1100200111	0203111101	0103330020	0001210410	1000100001	01001
<i>trifasciata</i>	101002111	1011100000	0000001001	0100200111	0203111101	0101110020	0001210410	1001000001	01001
<i>jenseni</i>	101110111	1001100000	0000101000	0100201111	0203111100	0101110020	0001210410	1001000000	01001
<i>snowi</i>	101110111	1001100000	00000001000	1100200111	0203111101	0102220020	0001210410	1001000001	01001
<i>bicellularis</i>	101002110	1111100000	0000101100	0100200111	0203111002	1100010020	6000011900	1000000201	01000
<i>europilosa</i>	101002111	1111100000	00001011?1	0100200111	0203111002	1103110021	0100010701	1100002200	01000
<i>mourei</i>	101002111	1111100000	0000001100	0100200111	0203111002	0103110021	0000010701	1100002200	00000
<i>similis</i>	101002111	1111100000	0000001101	0100200111	0203111002	0103110021	0000010701	1000000200	00000
<i>mellipes</i>	101002111	1111100000	0000001101	1100200111	0203111101	0022220021	0000010701	1100001200	01000
<i>campestris</i>	101002111	1111100000	0000101101	0000200111	0203111002	0122220021	0000010700	1100001200	01000
<i>tomentosa</i>	101002111	1111100000	0000001101	1200200111	0203111002	0100110021	0100010701	1100001200	01000
<i>pulchella</i>	101002111	1111100000	0000001111	1200200111	0203111002	?103220021	0000010701	1100001200	00000
<i>vernoniae</i>	101002111	1111100000	0000001111	1200200111	0203111101	1100030021	0000010701	1100001200	00000
<i>analis</i>	101002111	1111100000	0000001111	1200200111	0203111002	0003110021	0000010701	1100001200	00000
<i>bruesi</i>	101002111	1111100000	00001011?1	0200200111	0203111002	0003110021	0000010701	1100001200	00000
<i>fulvofasciata</i>	101002111	1111100000	0000101111	1200200111	0203111101	0021110021	0000010701	1100001200	01000

lopsis (*Phanomalopsis*) *jenseni* and related species, the two arms of the apical process of S-8 are much more complex than in other basal species of this clade, such as *E. solitaria* and *E. aureosericea*.

Stilbomalopsis is supported by five unique synapomorphies: the presence of apical bands on T-1 to T-4 of females (character 56-I); the subquadrangular disc of S-7 of males, whose lateral edges diverge toward the apex (character 60-

I; Fig.8b); the narrow, transverse apical sclerite of S-7 of males (character 6-I-I; Fig.8b, *ap*); the apical process of S-8 of males, which is composed of a single broad lobe separated from the disc by a long stalk (character 67-6; Fig.9e) and the ventral lobe of the penis valve (character 83-I; Fig.11b, *vl*). In some trees, character 67-6 is shown as a synapomorphy of *Stilbomalopsis* + *Diomalopsis*. This is not likely to be so, though, since *Diomalopsis* has character 67-9 instead. A ho-

moplastic character supporting this clade is lateral ocelli of female entirely below the summit of the head (character 13-0; Fig. 3a). This occurs, among other Exomalopsini, only in *Eremapis*.

The clade formed by *Exomalopsis s.s.* + *Megomalopsis* is supported by only one unique synapomorphy: the median elevated area of S-6 of males, which broadens toward the apex of the sternum, forming a carina or spine at each side (character 59-1). The long arms of the gonocoxite (character 71-1; Fig. 10, *ag*) are a unique feature of all *Exomalopsis s.s.* + *Megomalopsis*, except *E. similis*. In those topologies in which *E. similis* is not the first branch of this clade, this feature is shown as a unique synapomorphy for the group. When *E. similis* is the first branch, this feature is a synapomorphy of the rest of the clade. Similarly, the expansion of the apex of the gonocoxite, enclosing the base of the gonostylus (character 76-1; Fig. 14, *de, ve*), may be a synapomorphy of this clade. It is modified in *E. auropilosa*, *E. mourei* and *E. similis* and does not appear as a synapomorphy for the clade in topologies in which these species are the basal branches of the group.

Megomalopsis, represented by *Exomalopsis fulvofasciata* and *E. mellipes*, either appears as a polyphyletic lineage inside *Exomalopsis s.s.* (*sensu* Michener & Moure, 1957) or makes *Exomalopsis s.s.* paraphyletic and, thus, should not be retained as a taxonomic unit.

Diomalopsis is known from a single species and thus is characterized only by autapomorphic features. Its status as a subgenus of *Exomalopsis* may be retained, since it does not make any other group paraphyletic.

The clade comprising *Phanomalopsis s.s.*, *Stilbomalopsis*, *Diomalopsis* and *Exomalopsis s.s.* (from now on, *Exomalopsis s.l.*) is supported by two unique synapomorphies: the dorsal flange of the gonocoxite (character 70-1; Figs. 11a, and 14, *df*) and, in some trees, the lobe of the posterior (distal) margin of the bridge of the penis valves (character 79-1; Figs. 11a and 17a). This character, however, is reversed in *Exomalopsis s.s.* Other characters supporting that clade are: labrum and clypeus of male without yellow-pigmented areas (characters 16-0 and 17-0); propodeal articulating orifice directed downward on an oblique plane (character 26-1; Fig. 5d,e) and the central velvet-like pilose area of the basitibial plate of females (character 39-1). Characters 16-0 and 17-0 are the common state among the basal lineages of the bees included in this study, but appear nowhere else among the Exomalopsini (as defined above). Character 26-1 appears independently in the Eucerini. Character 39-1 curiously appears also in *Anthophoriscia pallidicornis*.

When all characters receive equal weights, two alternative hypotheses exist regarding the relationships among *Phanomalopsis*, *Stilbomalopsis* and *Diomalopsis* + *Exomalopsis s.s.* In the first hypothesis, *Diomalopsis* and *Stilbomalopsis* form a clade which is the sister group for another clade composed of *Phanomalopsis* and *Exomalopsis s.s.* (Fig. 21). In the second hypothesis, *Phanomalopsis* is the basal branch, followed by *Stilbomalopsis* and by *Diomalopsis* + *Exomalopsis s.s.* (Fig. 22). Among the trees generated after successive approxima-

tions, a third hypothesis (along with the second one) appears. In this third hypothesis, *Phanomalopsis* is sister to *Stilbomalopsis*, while *Diomalopsis* and *Exomalopsis s.s.* constitutes another lineage (Fig. 23).

In the first hypothesis, the sister group relationship between *Diomalopsis* and *Stilbomalopsis* is not supported by any unique character. Three features supporting this clade are the lack of punctuation and hairs on the disc of the first tergum of females (character 50-1) and the lack of tomentum on the marginal areas of T-2 and T-3 of females (characters 53-0 and 54-0). All of these occur in species of *Exomalopsis s.s.* The last character to support this clade is the lobe on the posterior margin of the dorsal bridge of the penis valves (character 79-1; Figs. 11a and 17a). This is also present in all *Phanomalopsis* and could well be a synapomorphy for all *Exomalopsis s.l.* that is reversed in *Exomalopsis s.s.*

In the same hypothesis, the sister group relationship between *Phanomalopsis* and *Exomalopsis s.s.* is supported by the excavation of the area between the lateral ocelli and the eyes of females (character 9-1; Fig. 1a,c), by the convex or flat vertex of females (behind the summit of head - character 11-1; Fig. 1c) and by the lack of a well delimited shining, non-punctate area above the propodeal pit of females (character 29-1). Character 9-1 is unique to these groups in Exomalopsini, but is present in other taxa like the Tapinotaspiini, *Melissodes* and *Tetrapedia*. Character 11-1 is present, among the species of *Phanomalopsis*, only in *Exomalopsis solitaria*. Character 29-1 is the most common condition in the outgroup taxa and is reversed in *Exomalopsis mourei*.

In the second hypothesis, the sister group relationship between *Stilbomalopsis* and the *Diomalopsis* + *Exomalopsis s.s.* lineage is supported by the following features: punctuation present on disc of T-I of female, between the dorsolateral convexities (character 50-1); and absence of tomentum on the marginal area of T-2 and T-3 of female (characters 53-0 and 54-0). Character 50-1 is not constant within *Exomalopsis s.s.* Characters 53-0 and 54-0 each occurs in only one species of *Exomalopsis s.s.*

In the third hypothesis, the sister-group relationship between *Phanomalopsis* and *Stilbomalopsis* is supported by the depression of the premarginal line of T-1 of females, forming a transverse sulcus (character 47-1), and by the expanded posterior margin of the dorsal bridge of the penis valves (character 79-1; Fig. 11a and 17a). Character 47-1 is also present in several species of *Exomalopsis s.s.* and in *Isoomalopsis*. Character 79-1 is also present in *Diomalopsis* and could be claimed, equally parsimoniously, to be a plesiomorphic feature of all four lineages of *Exomalopsis s.l.* that reversed in *Exomalopsis s.s.*

In the second and third hypotheses, the sister-group relationship between *Exomalopsis s.s.* and *Diomalopsis* is supported by two unique characters: the reduction of the disc of female T-1, which is less than one-third as long as the marginal area (character 49-2), and the short gonostylus that is triangular in profile, broader basally (character 77-2; Fig. 14).

The only relationship between any two groups among the lineages of *Exomalopsis* s.l. that is well supported is the one between *Diomalopsis* and *Exomalopsis* s.s. The positions of *Phaomalopsis* and *Stilbomalopsis* are not well defined.

Classificatory Proposals

The main concern while making classificatory decisions in this study was to be consistent with the phylogenetic hypothesis reconstructed for the groups involved (Hull, 1964). For this reason, only monophyletic taxa (*sensu* Hennig, 1966) were accepted. Whenever monophyly of groups was not violated, sinking established taxa or proposing new ones was avoided, so that taxonomic stability was maximized.

The first main classificatory change proposed here is the exclusion of *Chilimalopsis* and *Teratognatha* from the Exomalopsini, and the recognition of a new tribe for them. The acceptance of *Chilimalopsis* and *Teratognatha* as part of the Exomalopsini would make this tribe polyphyletic. Even considering that a sister-group relationship between those genera and Eucerini is not strongly supported, their unique synapomorphies justify a new tribe. Other changes presented here regard reformulation of the generic and subgeneric classification of Exomalopsini.

Tribe TERATOGNATHINI, new tribe

Minute and slender bees. Body black, except in males labrum and, in some cases, apical margin of clypeus yellow. Hairs generally sparse and short; scopa sparse, composed of minutely and sparsely branched hairs; maxillary palpus six-segmented (five-segmented in *Chilimalopsis impressifrons* and in male *Teratognatha modesta*); mandible with subapical tooth; labrum of female without median longitudinal line flanked by rows of erect hairs; clypeus weakly convex to weakly protuberant; internal margin of eye not margined by paracocular cilia; postocellar ridge absent; marginal cell obliquely truncate apically (round, separating from wing margin in a gentle curve in *Chilimalopsis* sp.), longer than distance between its apex and wing tip; pterostigma small, less than three times as long as prestigma (longer in *Teratognatha*), its margin, inside marginal cell, straight or gently convex; pygidial plate present in females and in male *Chilimalopsis* sp., indicated by transverse recurved carina in male *C. impressifrons* and absent in *Teratognatha*; S-7 of male pentagonal; anterior edge of S-8 of male pointed; internal wall of gonocoxite with peglike setae, subapically, and narrow apical process above gonostylus and directed dorsad; gonostylus relatively long and slender, originating in apicolateral projection of gonocoxite and extending in an axis parallel to that of gonocoxite. Restricted to the semi-arid regions of Argentina and Chile and, perhaps, Bolivia and Paraguay.

Two genera are currently recognized in this tribe: *Teratognatha* Ogloblin (containing a single species, *T. modesta* Ogloblin) and *Chilimalopsis* Toro (containing *C. parvula* Toro and *C. impressifrons* Roig-Alsina). It seems that the species referred to as *Chilimalopsis* sp. in this paper is an additional undescribed species from Chile. In the analyses above *Chilimalopsis impressifrons* appeared to be more closely related to *Teratognatha modesta* than to *Chilimalopsis* sp., which renders the genus *Chilimalopsis* paraphyletic. For this reason, the generic classification of the Teratognathini is not treated here, but will be subject of a separate detailed study.

Tribe EXOMALOPSINI

Taxonomy: Michener, 1944:271; Michener & Moure, 1957:405; Michener, 1974:23,28; 1979:278,287,314,332,333,335; Hurd, 1979:2115; Roig-Alsina & Michener, 1993:155; Silveira, 1993.
Biology: Rozen, 1984.

Minute to small bees, generally robust. Body black, except for yellow labrum and clypeus of *Eremapis* and of male *Anthophorula* s.l. and for red metasoma in some *Anthophorula* and *Exomalopsis*. Hairy, pubescence often long; scopa dense, composed of long hairs coarsely plumose to apices. Maxillary palpus six-segmented (five-segmented in *Eremapis*); labrum of females (except in some *Phaomalopsis*) with a median longitudinal line, sometimes elevated, flanked by rows of erect hairs; mandible (except in *Eremapis*) simple, without subapical tooth; clypeus flat or weakly convex; internal margin of eye (except in *Eremapis*) margined by paracocular cilia; postocellar ridge absent or present; marginal cell obliquely truncate apically, longer than distance between its apex and wing tip; pterostigma large (short in *Anthophorula* s.s.), its margin, inside marginal cell, gently convex or truncate; pygidial plate present in females and in males of *Anthophorula* s.s., absent on male *Eremapis*, suggested by an apical recurved carina in male *Isomalopsis*, *Anthophorisca* and *Exomalopsis* s.l.; shape of S-7 of males variable but not pentagonal; anterior edge of S-8 of male straight or broadly convex medially (pointed in *Eremapis*); internal wall of gonocoxite simple, without apical process (except in *Exomalopsis solitaria* and *E. aureosericea*) or peglike setae subapically; gonostylus variable in shape, but always originating on the apex of gonocoxite and extending in the same axis as gonocoxite. Mostly neotropical, occurring from northern Argentina to western and central U.S.A.

Genus *Eremapis* Ogloblin

Eremapis Ogloblin, 1956:149; Michener & Moure, 1957:405,435; Roig-Alsina, 1992:152. Type species: *Eremapis parvula* Ogloblin, 1956 (original designation).

This genus was well described by Ogloblin (1956) and again by Michener & Moure (1957). It consists of a single species, *E. parvula*, from Argentina.

Genus *Anthophorula* Cockerell

Anthophorula is again raised to generic rank. Here, however, it is expanded to include not only the North American *Anthophorula* s.s. and *Anthophorisca*, but also the South American *Isomalopsis*. The close affinity between *Isomalopsis* and *Anthophorula* was already noted by Michener & Moure (1957).

Labrum and clypeus of male yellow (except in *Anthophorisca levi-gata* and *A. linsleyi*); area between lateral ocellus and eye convex; postocellar ridge absent; superior margin of eyes below level of summit of head in *Anthophorisca*, above in *Isomalopsis* and most *Anthophorula* s.s.; basitibial plate of female small, its surface flat and uniformly hairy (except in *Anthophorisca pallidicornis* as in *Exomalopsis*); transverse carina of T-1 of female present (weak or sometimes absent in *Anthophorisca*), that of male present in *Anthophorula* and *Isomalopsis*; disc of S-7 of male bilobed, much broader than long (in *Isomalopsis* base of lobes broadened and apodemes reduced); penis valves narrow, dorsal edges closer to each other than ventral ones (except in *Isomalopsis*); dorsal flange of gonocoxite absent.

Subgenus *Isomalopsis* Michener & Moure (new status)

Isomalopsis Michener & Moure, 1957:405,434. Type species: *Tetralonia niveata* Friese, 1908 (original designation).

This subgenus was described and illustrated by Michener & Moure (1957) as a separate genus. It is currently known from a

single species, *I. niveata*, from Argentina. I have seen specimens identified by Moure as belonging to a second undescribed species. I did not make a detailed comparison between it and *I. niveata* and, without detailed study, I could not distinguish it from *I. niveata*.

Subgenus *Anthophorula* Cockerell *sensu stricto*.

Anthophorula Cockerell, 1897:44; 1898:42,70; Lutz & Cockerell, 1920:564; Michener, 1951: 1187; Michener & Moure, 1957:432; Hurd, 1979:2116; Timberlake, 1980:3-37,43. Type species: *Anthophorula compactula* Cockerell, 1897 (original designation).

Diadasiella Ashmead, 1899:64. Type species: *Diadasiella coquillettii* Ashmead, 1899 (= *Synhaloma albicans* Provancher) (original designation and monobasic).

Pachycerapis Cockerell, 1922:4. Type species: *Exomalopsis (Pachycerapis) cornigera* Cockerell, 1922 (original designation and monobasic).

This group is well characterized in Michener & Moure (1957) as *Exomalopsis (Anthophorula)*. Timberlake (1980) recognized 29 species in this subgenus and provided a key for their identification. Species of *Anthophorula* occur in Mexico from Hidalgo and Jalisco northward into the U.S.A., to Oregon in the west and Texas in the east.

Subgenus *Anthophorisca* Michener & Moure

Anthophorisca Michener & Moure, 1957:433; Hurd, 1979:2118; Timberlake, 1980:39-73. Type species: *Melissodes pygmaea* Cresson, 1872 (original designation).

Panomalopsis Timberlake, 1980:82. Type species: *Exomalopsis linsleyi* Timberlake, 1980 (original designation). New synonym.

This group is well described in Michener & Moure (1957), and a useful key for its species is provided by Timberlake (1980). This group includes the subgenus *Panomalopsis*, erected by Timberlake (1980) for *Exomalopsis linsleyi*. This species is known only from the male holotype and, for this reason, was not included in the phylogenetic analyses. I have examined the type specimen and regard it as being a derived *Anthophorisca*. With the inclusion of *A. linsleyi*, *Anthophorisca* comprises 30 species. Species of *Anthophorisca* occur from Oaxaca, in Mexico, northward into the U.S.A., to California in the west, Indiana and Mississippi in the east, and Nebraska in the north.

Genus *Exomalopsis* Spinola

Exomalopsis Spinola, 1853:89; Smith, 1854:364; 1879:125; Taschenberg, 1883:82; Dalla Torre, 1896:298; Cockerell, 1898:42,71; Friese, 1899:247; Ashmead, 1899:64; Schrotky, 1902: 525; 1913:262; Ducke, 1906:59; 1912:97; Brèthes, 1909:223; Lutz & Cockerell, 1920:564; Michener, 1941:301; 1944:272; 1951:1187; 1974:28; 1979:314,317,334,336; Michener & Moure, 1957:405, 427; Timberlake, 1947, 1980; Mitchell, 1962:235; Michener *et al.*, 1994: 158.

The scope of this genus is restricted here by the exclusion of *Anthophorula* and *Anthophorisca*. Its species can be characterized by the following set of features:

Labrum and clypeus of male dark as in female; pterostigma large, two-thirds as long as marginal cell on wing margin or more, its apex sometimes truncate; basitibial plate of female large, with central pilose area separated by groove from raised margin; transverse carina of T-1 present on females, absent from males (except in some *Phanomalopsis*); premarginal line of T-1 of female evident or not, sometimes depressed, forming groove; S-7 and S-8 and genitalia of male highly variable, dorsal flange of gonocoxite present.

Subgenus *Stilbomalopsis* new subgenus

Type species: *Exomalopsis solani* Cockerell, 1896.

This group of species was included by Michener & Moure (1957) in their subgenus *Phanomalopsis* and was considered as such by Timberlake (1980). It can be characterized by the following set of features:

Small, robust, hairy bees. Body black. Labrum flat with apical margin gently curved (except in *arcuata*, in which the surface is slightly concave and the margin pointed); clypeus flat; vertex in frontal view convex; area between lateral ocelli and eye not excavated (except in *arcuata*), bare and shining or with minute punctures and hairs; superior margin of eye below level of vertex behind it; postocellar ridge absent; propodeum with large well-defined shining area medially; pterostigma large (at least three times as long as prestigma), generally truncate apically; disc of T-1 of female one-third as long as marginal zone or more; disc of T-1 and marginal zones of T-1 and T-2 (sometimes also T-3 and T-4) bare, impunctate and shining; apical fimbria of T-2 to T-4 dense and soft, generally white, sometimes interrupted medially. S-6 of male entirely flat; disc of S-7 of male subquadrangular, its lateral edges arcuate, closest to each other medially; ventral lobe of penis valve present; apical process of S-7 of male present as narrow transverse sclerite fused laterally to arms of disc; apical process of S-8 of male a single bare lobe.

Eleven of the species listed by Timberlake (1980) as *Phanomalopsis* belong in this group (*affabilis* Timberlake, *arcuata* Timberlake, *binotata* Timberlake, *birkmanni* Cockerell, *byersi* Timberlake, *dimidiata* Timberlake, *hurdii* Timberlake, *limata* Cresson, *pueblana* Timberlake, *solani* Cockerell, *solidaginis* Cockerell). Among these, *arcuata* is unusual for the excavated area between the lateral ocellus and eye and for the concave, pointed labrum of the female. The male also has unusual features on S-7 and S-8 as well as in the gonocoxite. Additionally, *aequalis* and *notabilis*, probably fit here. *Exomalopsis bakeri* seems to be an *Exomalopsis* *s.s.* The species of *Stilbomalopsis* can be identified with the help of Timberlake's key. *Stilbomalopsis* occurs in Central America, from El Salvador and Nicaragua, northward through Mexico to California, Arizona, New Mexico and Texas in the U.S.A.

Etymology: from the Greek words *stilbo* (glitter, shine); *homas* (flat); *opsis* (face). "A shining *Exomalopsis*". The name refers to the smooth and shining abdominal terga.

Subgenus *Phanomalopsis* Michener & Moure

Phanomalopsis Michener & Moure, 1957:430; Hurd, 1979:2116; Timberlake, 1980:79,83. Type species: *Exomalopsis jenseni* Friese, 1908 (original designation).

This subgenus is restricted here, compared to its definition by Michener & Moure (1957), by the removal of *Exomalopsis solani* and related species to *Stilbomalopsis*. Three grades can be identified in *Phanomalopsis*. One is composed of two small species, *E. solitaria* and *E. diminuta*; another by *Exomalopsis aurosericea*, *E. trifasciata* and *E. atlantica*; and the third by *Exomalopsis jenseni* and related species. Only the third group is supported as a monophyletic assemblage by synapomorphic features. The first two groups retain many plesiomorphic features which make this subgenus difficult to characterize without using male genitalia.

Labrum and clypeus of male dark; vertex of head of females, in frontal view, in straight lines; lateral ocelli above summit of head; area between lateral ocelli and eye broad, gently excavated (more so in males); postocellar ridge absent or very weakly developed; superior margin of eyes of females below (sometimes almost at the same level as) summit of head behind it; premarginal line of T-1 of female depressed, forming groove; disc of T-1 of female punctate and pilose (sometimes only partially), at least one-third as long as marginal area; marginal area of T-1 of female glabrous and shining, except sometimes for area behind dorsolateral convexities. S-6 of male entirely flat; apical process of S-7 complex, with two

basi-lateral lobes on the ventral surface; apical process of S-8 produced into two long arms, sometimes with hairs and complex accessory lobes.

Phanomalopsis comprises 10 species. Most of them occur in the pampa and semidesertic areas of northern Argentina, Bolivia and Paraguay. A single species, *E. (P.) snowi* occurs from the Caribbean coast of Venezuela and Colombia, through Panamá, Guatemala, Mexico to southern Texas in the U.S.A. A small group of species exists in southern and southeastern Brazil. No species is known to occur in the savannas of central Brazil or in the Amazonian basin.

Subgenus *Diomalopsis* Michener & Moure

Diomalopsis Michener & Moure, 1957:431. Type species: *Exomalopsis buclularis* Michener & Moure, 1957 (original designation).

This group was well described by Michener & Moure (1957) and is known from a single species which occurs only in the Atlantic Forest on the southeastern Brazilian coast. An additional undescribed species from eastern Paraguay and southwestern Brazil seems to fit in this subgenus. I have seen only females of this species and an examination of male genitalia would be necessary to confirm its position.

Subgenus *Exomalopsis* Spinola *sensu stricto*

Exomalopsis Michener, 1951:1187; Michener & Moure, 1957:428; Urd, 1979:2115; Timberlake, 1980:119. Type species: *Exomalopsis auripilosa* Spinola, 1853 [by designation of Taschenberg, 1883:82 (as *E. fulvopilosa*)].

?*Epimomispractor* Holmberg, 1903:426. Type species *Epimomispractor gratiosus* Holmberg, 1903 (original designation).

Megomalopsis Michener & Moure, 1957:430; Timberlake, 1980:79, 101. Type species *Exomalopsis diversipes* Cockerell, 1949 (original designation). New synonym.

This group is redefined here to comprise the species placed by Michener & Moure (1957) and Timberlake (1980) in both *Exomalopsis* *s.s.* and *Megomalopsis*.

Outline of summit of head, in frontal view, between lateral ocellus and eye, straight; area between lateral ocellus and eye excavated; postocellar ridge present (sometimes limited to area just at sides of lateral ocelli); area above propodeal pit punctate as rest of propodeum (shining in *mourei*); disc of T-1 of female less than one-third as long as marginal zone; S-6 of male with median elevated area broadening toward apex, forming carina or spine at each side; disc of S-7 of male subtriangular with no apical process; apical process of S-8 short, produced as two apical projections; gonocoxite long, almost reaching tips of penis valves; gonostylus arising from an invagination produced by expansion of apex of gonocoxite; dorsal flange placed apically on gonocoxite.

This is the most speciose group of Exomalopsiini and the one whose species-level taxonomy is least studied. There are about 50 valid species in this subgenus (Silveira, 1995). A revision of this group, however, will certainly reveal new synonymies and new species. It occurs from northern Argentina to southwestern U.S.A., both in semidesertic and forested areas. The last comprehensive study to consider the faunas of all the Americas together was that of Friese (1899). Timberlake (1980) reviewed the species of North and Central America, but his work is badly in need of revision. Furthermore, his key was published with many mistakes which make it almost impossible to use. After Friese's (1899) paper no revision was made of the South American species, but new species were described in innumerable isolated papers or in accounts of regional bee faunas. The location of the types of several of these is currently unknown.

KEY TO THE GENERA AND SUBGENERA OF EXOMALOPSINI

(Note: this key ends in a triplet instead of a couplet).

1. Second medial cell of forewing about as long as second cubital; labrum and clypeus of female yellow; T-7 of male produced into a broad sharp carina; S-7 of male trilobed *Eremapis*.
- Second medial cell of forewing distinctly shorter than second cubital; labrum and clypeus of female entirely dark; margin of T-7 of male not produced into a carina, or if a carina is present, then its posterior margin is recurved; S-7 of male not trilobed 2
2. Basitibial plate of female with surface flat; if margins of plate are raised, then transverse carina of T-1 of female absent; labrum and clypeus of male yellow or white [except in *Anthophorula* (*Anthophorisca*) *levigata* and *A. (Anthophorisca)* *linsleyi*]; outer side of penis valve without lateral process; dorsal flange of gonocoxite absent (*Anthophorula* *s.l.*) 3
- Basitibial plate of female with raised margin (generally separated from central pilose area by groove); transverse carina of T-1 of female present; labrum and clypeus of male entirely dark; outer side of penis valve with lateral process; dorsal flange of gonocoxite present (*Exomalopsis* *s.l.*) 5
3. Transverse carina of T-1 of female weak or absent; that of male absent; peglike setae present on apex of gonocoxite (except in *A. linsleyi*, which has strong pointed setae instead) *Anthophorisca*.
- Transverse carina of T-1 of female strong; that of male present; peglike setae absent from apex of gonocoxite 4
4. Pterostigma large, 4 times as long as prestigma, its inner breadth much greater than breadth of its marginal veins; yellow marks on clypeus of male absent or restricted to an apical transverse line; S-6 of male with two lateral flanges which bear a series of spicules on their inner margins *Isomalopsis*.
- Pterostigma small, no more than 3 times as long as prestigma, its inner breadth as large as or smaller than breadth of its marginal veins; clypeus of male entirely yellow; S-6 of male simple *Anthophorula* *s.s.*
5. Vertex in frontal view convex; area between lateral ocellus and eye not excavated (except in *E. arcuata*) and lateral ocelli below level of summit of head; marginal zones of T-1 and T-2 of female smooth and glabrous; T-2 to T-4 of female with white, dense, apical fasciae, sometimes interrupted medially; apical process of S-7 of male present as narrow transverse sclerite fused laterally to arms of disc; apical process of S-8 of male a single bare lobe *Stilbomalopsis*.
- Vertex in frontal view straight; area between lateral ocellus and eye excavated and/or lateral ocelli above level of summit of head; marginal zone of T-1 and/or T-2 of female punctate and pilose; T-2 to T-4 of female with apical fasciae absent or present; apical process of S-7 of male absent or complex and with two free

- basilateral lobes under ventral surface; apical process of S-8 bearing two apical arms (short or long); *if* a single broad lobe, than lobe is hairy 6
6. Three submarginal cells; vertex of female between ocellus and eye gently excavated (more so on males); postocellar ridge absent (but summit of head sometimes narrow); premarginal line depressed on T-1 of female, forming transverse sulcus, *and* marginal zone between dorsolateral convexities smooth and shining, comprising no more than two-thirds of dorsal surface of tergum; S-6 of male entirely flat *Phanomalopsis*.
- Three submarginal cells; vertex of female between ocellus and eye excavated; postocellar ridge present, sometimes limited to portions just to sides of lateral ocelli; *if* premarginal line depressed on T-1 of female, then marginal zone between the dorsolateral convexities punctate *and/or* comprising much more than two-thirds of dorsal surface of tergum; S-6 of male with median elevated area that broadens toward apex of sternum, forming a carina or spine at each side; S-7 and S-8 of male without peg-like setae *Exomalopsis* s.s.
- Two submarginal cells; vertex of female between ocellus and eye not excavated; postocellar ridge absent; premarginal line on T-1 of female not depressed; S-6 of male entirely flat; S-7 and S-8 of male with peg-like setae *Diomalopsis*.

DISCUSSION AND CONCLUSIONS

Phylogenetic Considerations

The understanding of the relationships among the taxa formerly included in the Anthophoridae has recently changed greatly. The scope of Exomalopsini was greatly modified by Roig-Alsina & Michener (1993) and by the removal of the Teratognathini in this paper. Changes have been drastic enough to make meaningless previous statements (*e.g.*, Michener, 1944; Michener & Moure, 1957) about Exomalopsini being the most primitive branch of the Anthophorinae (*sensu* Michener, 1944;) or the Apinae (*sensu* Roig-Alsina & Michener, 1993). The results obtained here offer a new hypothesis for the relationships of Exomalopsini. As redefined here, Exomalopsini would not be the most primitive branch of Apinae, but the sister taxon of a group including Ancylini, Eucerini and the newly proposed Teratognathini.

The Ancylini, once suspected to be closely related to or part of the Exomalopsini, (Michener, 1944; Michener & Moure, 1957; Silveira, 1993) appears here to be more closely related to the Eucerini. This was already suggested by Roig-Alsina & Michener (1993). *Tarsalia* appeared at the base of Eucerini in some of the trees obtained by those authors, who argued that the Ancylini could indeed be a basal branch of the Eucerini. Here, the monophyly of the Ancylini receives additional support and Teratognathini is hypothesized to be the sister-group of the Eucerini. The relationship of Ter-

atognathini to Eucerini, however, is not strongly supported.

Exomalopsini as here defined contains three genera: *Eremapis*, *Anthophorula* (with the subgenera *Anthophorula* s.s., *Anthophorisca* and *Isomalopsis*) and *Exomalopsis* (with the subgenera *Exomalopsis* s.s., *Diomalopsis*, *Phanomalopsis* and *Stilbomalopsis*).

Relationships among the subgenera of *Anthophorula* were consistent throughout the analyses: *Anthophorisca* is the sister-group of a clade composed of *Isomalopsis* and *Anthophorula* s.s. *Panomalopsis linsleyi* Timberlake is considered to be a highly derived *Anthophorisca* and is included in that subgenus.

The subgenera of *Exomalopsis* are consistent groups. Only *Phanomalopsis*, with a few basal species that retain many of the plesiomorphies for the clade, cannot be sharply separated from the others. It seems quite possible that *Diomalopsis* and *Exomalopsis* s.s. are sister taxa, but the relationships between them and the other subgenera are not clear.

Biogeographic Considerations

The idea of a close relationship between Ancylini and Exomalopsini (*e.g.* Michener, 1944; Michener & Moure, 1957) posed a biogeographic puzzle: Ancylini are restricted to the xeric strip of land extending from the Mediterranean basin to central Asia, while Exomalopsini are restricted to the western hemisphere. The phylogenetic hypothesis resulting from the present analyses transfers the biogeographic puzzle from the relationship between Ancylini and Exomalopsini to the relationships among a greater number of taxa. The topology for the tribes of Apinae employed as outgroups shows successive branches alternating between groups currently occurring in the western and eastern hemispheres and does not seem to contribute to the elucidation of the biogeographical history of the subfamily.

The phylogenetic relationships among the groups of Exomalopsini as defined here and their geographical ranges suggest a complex biogeographic history that may include major vicariant events along with dispersal through xeric corridors in past drier times in the Americas.

Eremapis, the most basal extant lineage of Exomalopsini, is restricted to temperate South America. This supports the belief of a South American origin for the tribe (Michener, 1944, 1979; Michener & Moure, 1957). However, it is possible that *Eremapis* is just a remnant of a once widespread lineage. The sister-group relationship between *Isomalopsis* and *Anthophorula* s.s. suggests that the ancestral stock of *Anthophorula* was widespread throughout the Americas at a time in which xeric climates were prevalent. Other examples of bee taxa presenting this amphitropical distribution are, according to Michener (1979), the genera and subgenera *Ptilothrix* and *Dasiapis* (Emphorini), *Martinapis* (Eucerini) and *Xerocentris* (Centridini). The existence of several amphitropical taxa occurring in xeric areas of both temperate regions of the Americas suggests one or more major opportunities for faunistic interchange between the southern and the northern continents. It has already been suggested that part of this interchange might have occurred before

the union of the Americas (Michener, 1979).

Among the lineages of *Exomalopsis*, *Stilbomalopsis* is restricted to Central and North America northward to south-western United States and probably originated there. Most species of *Phanomalopsis*, including its basal lineages, are in South America and this is probably where they originated. The origin of *Exomalopsis* s.s., however, is less clear, since there is not a consensus hypothesis about the basal branches in the lineage. Acceptance of a sister-group relationship with *Diomalopsis* would suggest a South American origin for the group.

The results of the phylogenetic analyses suggest a semi-desertic habitat for the ancestral species of Exomalopsini. They suggest also that invasion of other habitats occurred relatively recently in the history of the tribe and has happened independently at least twice: once or more in *Phanomalopsis* and again in *Exomalopsis* s.s. *Eremapis* (the most basal lineage of the tribe), *Anthophorula* s.l. and the most basal lineages of *Exomalopsis* s.l. are mostly restricted to semi-desertic areas: *Eremapis* and *Isomalopsis* in temperate South America; *Anthophorisca*, *Anthophorula* and *Stilbomalopsis* in similar habitats in North America. Most *Phanomalopsis*, including one of its most basal extant species (*E. solitaria*), are restricted to arid areas (although other basal species, *E. au-rosericea* and *E. atlantica*, live in forested habitats). Only *Diomalopsis* and most species of *Exomalopsis* s.s. are restricted to moist tropical environments.

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